The Soil Moisture Niche in a Moist Tropical Forest – A Demographic Approach

Von der Fakultät für Lebenswissenschaften

der Universität Leipzig

genehmigte

D I S S E R T A T I O N

zur Erlangung des akademischen Grades

doctor rerum naturalium

(*Dr. rer. nat.*)

vorgelegt

von

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geboren am 11. November 1989 in Nieuwegein, Niederlande

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Leipzig, den 17. Januar 2020

(Tag der Verteidigung)

BIBLIOGRAPHISCHE DARSTELLUNG

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Fakultät für Lebenswissenschaften

Universität Leipzig

Dissertation

229 Seiten, 410 Literaturangaben, 52 Abbildungen, 7 Tabelle

Synopsis

Water availability affects tree species performance and distributions in tropical forests. However, there are no studies that have measured detailed spatial variation in soil water availability within a tropical forest. This limits our understanding of how water availability shapes the demography and distributions of tree species within tropical forests. In this dissertation, I measured detailed spatial variation in soil water potential (SWP), the relevant measure of water availability for plant performance, in the seasonal tropical moist forest of the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama. In Paper 1, I mapped spatial variation in SWP across the 50-ha plot in various stages of the dry season using information on topography, soil type, dry season intensity and more. In Paper 2, I quantified the soil moisture niches of species in terms of demographic responses (growth and mortality) and species distributions. I related seedling growth and mortality responses to SWP of 62 species to their distributional centre along the SWP gradient, using data from 20 years of annual seedling censuses across 200 seedling census sites. I found that species that grew faster (slow) with increasing SWP were more common on wetter (drier) parts of the SWP gradient. Moreover, wet-distributed species grew faster on the wet side of the SWP gradient than dry-distributed species. Mortality was unrelated to species distributions but decreased strongly with seedling height. These findings indicate that species with a growth advantage with respect to SWP grow faster out of the vulnerable small size ranges, reducing their mortality in later seedling stages and thus shaping species distributions indirectly. This mechanism is a form of niche differentiation that contributes to species coexistence. In Paper 3, I related seedling growth and mortality responses to spatiotemporal variation in water availability with responses to light availability, another highly limiting resource in tropical forests. I found an interspecific trade-off in responses to shade versus inter-annual drought (dry season intensity): species that performed relatively well in the shade performed worse during more severe dry seasons and vice versa. This trade-off enables coexistence, because species are adapted to perform well under either shade or drought. In sum, water availability contributes to the maintenance of the high diversity of tropical forests through hydrological niche differentiation and a trade-off between performance in shade versus drought. Future work can use my SWP maps and species responses to SWP to identify the functional traits that underlie the species responses and improve Dynamic Global Vegetation Models. Finally, my work facilitates the prediction of future species composition, diversity and ecosystem functioning of tropical forests with shifts in rainfall patterns caused by climate change.

ACKNOWLEDGEMENTS

I have received support from many people during this journey of pursuing my PhD degree. I want to thank my daily supervisor, Nadja Rüger, for the very abundant help and support. I also thank Christian Wirth, my official supervisor, for many in-depth discussions and advice. Together, Nadja and Christian have made this dissertation possible by helping me wherever necessary.

I also owe much to Bettina Engelbrecht, who was a very valuable member of my PhD Advisory Committee (PAC) and helped me to get the fieldwork done smoothly, which enabled me to obtain all soil moisture data on which this thesis is based. I am also grateful to Joe Wright for providing me access to the seedling data, another crucial dataset of my thesis, as well as for for many constructive comments and for hosting me at Princeton University. I thank the other co-authors of my papers, Andrés Hernández and Richard Condit, for data and comments. I also thank all reviewers and editors of my papers for making my work better.

I wish to thank Alexandra Weigelt for providing me with fieldwork equipment and the entire AG Wirth for providing me the chance to present my work in their seminars and inviting me to their annual retreat. I thank Anke Hildebrandt for helping me preparing my sampling campaign. I also thank STRI for funding and all STRI staff, in particular Oris Acevedo and Hilda Castaneda, for hosting me on Barro Colorado Island. I thank Angel Guardia, Ariel Miranda, Daniel González, Estibali Wilkie and Leida Pérez for the hard work in the field and the laboratory.

I thank iDiv and the DFG for funding my project. I thank everyone at iDiv for the many discussions and the good time I had at the institute. I thank yDiv, in particular Mari Bieri, Godefroy Devevey, Nicole Sachmerda-Schulz and Johanna Müller, for the great retreats and courses, the help with organising my PAC meetings and the general support.

Finally, I am grateful to my family and friends for supporting me during my PhD. Most of all, I want to thank my partner, Darina Iskreva, for always being by my side and supporting me no matter what, not to mention the great help she gave me during the fieldwork. Without her help this project would not have been what it is now.

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SUMMARY

Water availability strongly affects tree species performance and distributions in tropical forests. Among regions, differences in the amount and seasonality of rainfall determine the distribution of tree species. Locally, species distributions are often associated to topographic or edaphic habitats that vary in soil water availability. Observational studies and experiments across and within tropical forests show that growth and mortality rates of species are affected by seasonal and inter-annual (e.g. El Niño) droughts. However, measurements of soil water availability within tropical forests are scarce, limiting our understanding of how soil moisture affects individual species and how it thereby shapes local species distributions, composition and diversity. At the same time, it remains unclear how the effect of water availability on tropical tree communities interacts with another highly limiting resource in tropical forests: light availability.

In this dissertation, I studied the roles of soil moisture and light availability in shaping the tree species community in a tropical moist forest on Barro Colorado Island (BCI), Panama. The aim of my dissertation was twofold. The first aim was to determine how soil moisture shapes local tropical tree species communities in terms of species demography and distributions. The second aim was to determine the relationship between species performance with respect to water and light availability. To do this, I (1) quantified spatial variation in soil moisture in a seasonal tropical moist forest, (2) determined the demographic mechanisms by which soil moisture shapes local tree species communities and (3) studied the relationship between the effects of water and light availability on species demography. I tackled these three tasks in the three papers of my dissertation, and I synthesised the findings of these papers in the general discussion.

I ground my work in niche theory, because it postulates that separation of species distributions along resource gradients such as water availability (i.e. niche differentiation) contributes to the high diversity in tropical forests. I define the niche in two ways; as the (1) performance and (2) distribution of species with respect to resources (here: water and light availability). I focus on realised niches as opposed to fundamental niches, because I study species in their natural environment where they encounter competitors. I specifically focus on the regeneration niche, because I study the demography and distributions of seedlings.

SUMMARY

The first step of my dissertation was to measure soil water availability in the 50-ha Forest Dynamics Plot in the seasonal tropical moist forest on BCI, which is the oldest and best-studied permanent forest plot in the global CTFS-ForestGEO monitoring network. I measured soil moisture in the regular dry season of 2015 and the severe dry season of 2016, which was associated with a strong El Niño drought. I measured both soil water content (the percentage of water in the soil) and soil water potential (a measure of how freely water can move in the soil, e.g. be taken up by plants). I focus my work on soil water potential (SWP), because it is most relevant for plant functioning as plants take up water along a soil-plant-atmosphere continuum of water potential. In total, I took 1380 soil moisture samples at 363 locations in the plot, making my dataset the most detailed soil moisture dataset within a permanent tropical forest plot. I used these data to map soil moisture across the 50-ha plot (Paper 1) and determine its effect on the growth, mortality and distributions of seedlings (Paper 2 and 3), which were censused annually for 20 years at 200 seedling census sites across the 50-ha plot.

In Paper 1, I quantified spatial variation in soil water availability in the 50-ha plot on BCI. I mapped SWP for the entire 50-ha plot based on my soil samples. I used a machine learning method called Random Forest, because it could handle my uneven spatial sampling design. I sampled unevenly across the plot because of restrictions to reduce potential damage to the vegetation. In order to map SWP across the plot, I used various spatial predictors such as topography and soil type. I also used temporal predictors such as the time of sampling and the intensity of the dry season at the moment of sampling, which I based on soil moisture monitoring data from a nearby location on the island. As expected, SWP decreased (i.e. soils were drier) when the dry season was more severe, soils were sandy and slopes were shallow. In addition to the maps, I provided R code that users can adapt to create custom maps for varying dry season intensities. These maps can be used in future studies on species demography, distributions, composition and diversity as well as ecosystem functioning under current and future climate conditions.

In Paper 2, I studied the demographic mechanism by which soil moisture shapes local tree species distributions. I expected that increased seedling performance (growth or mortality) of species at high or low SWP would cause their species distributions to be associated to high or low SWP, respectively. I found that growth responses to SWP were positively related to species distributions: species that performed better at higher (lower) SWP occurred more frequently at

higher (lower) SWP. Moreover, I found that wet-distributed species not only grew faster 'at home' (in wetter sites), but also had a 'home advantage', i.e. they grew faster than dry-distributed species in wetter sites. Mortality responses to SWP were unrelated to species distributions. Instead, mortality decreased strongly with seedling size; taller seedlings had much lower mortality than smaller seedlings. Thus, a growth advantage indirectly affected species distributions by allowing species with a growth advantage with respect to soil moisture to escape small sizes quicker, reducing their mortality.

I found that more species had significantly restricted distributions than expected at random compared to species with widespread distributions. This provides evidence for niche differentiation, because species distributions were more often constrained to specific parts of the SWP gradient as opposed to being widespread. In addition, species distributions along the SWP gradient remained constant across life stages from seedlings to saplings and trees, which was not found in earlier studies that looked at topographic habitat associations. Surprisingly, I found relatively few significant growth and mortality responses to SWP. There are several possible reasons for this. First, the SWP gradient was relatively shallow because of the relatively flat topography on BCI, limiting differences in species responses to SWP. Second, dispersal limitation likely prevented moisture-sensitive species to reach unfavourable sites and thereby also limited the range of SWP that species experience. Third, species had relatively small sample sizes, which increased uncertainty in their responses. There were also relatively few significant distributional associations to the SWP gradient. This was particularly the case when I corrected for species clumping and spatial autocorrelation, indicating that dispersal limitation shapes species distributions by creating clumps of species that are not associated with the SWP gradient. Taken together, my findings indicate that variation in SWP causes niche differentiation on BCI, albeit relatively subtly (i.e. for few species). Moreover, detailed soil moisture measurements are needed to discover the mechanisms by which water availability shapes species communities, because earlier studies that lacked these data did not find the link between growth and distributions nor did they find consistent of distributional associations to habitats.

In Paper 3, I studied the relationship between the effects of water and light availability on seedling demography. I related seedling growth and mortality responses of species to spatial drought (i.e. the inverse of SWP) and inter-annual drought (the maximum cumulative water deficit,

i.e. the intensity of the dry season) to species responses to spatiotemporal variation in shade (a shade index based on the presence or absence of vegetation above all 200 seedling census sites for 20 years. I expected a trade-off between responses to shad and drought, because I expected a trade-off in allocation between above-ground and below-ground structures to capture light and water, respectively. I found a trade-off between responses to shade and inter-annual drought, indicating that the ability of species to perform well in the shade comes at the cost of coping with droughts and vice versa. The shade-drought response trade-off emerged from the absence of species that performed particularly well or poorly in both shade and drought. Additionally, the trade-off was likely reinforced by the fact that light availability is higher during droughts and in drier sites, allowing shade sensitive species to perform well during droughts and drought sensitive species to perform well in the shade.

Surprisingly, there was no relationship between responses to shade and spatial drought. The absence of a relationship may be due to the relatively weak effect of spatial drought on performance. As in Paper 2, possible reasons for this are the relatively shallow SWP gradient, dispersal limitation and relatively low sample sizes, limiting demographic responses of species to SWP. In contrast, shade affected growth and inter-annual drought affected survival for a large percentage of species. My work suggests that shade and inter-annual droughts affect species performance more strongly than spatial variation in soil moisture. However, definitive conclusions on the relative importance of shade and drought for species performance cannot be drawn because sample sizes differed for shade and drought responses: shade was only measured in half the years with seedling censuses, which prevented me from including particularly shade-sensitive species in my analysis.

In this dissertation, I showed that (1) spatial variation in SWP is most strongly related to soil type and topography, (2) growth responses to SWP shape species distributions indirectly through mortality and (3) demographic responses to inter-annual drought (but not spatial drought) trade off with responses to shade. I discovered a novel mechanism by which spatial variation in soil moisture shapes species distribution and thereby leads to niche differentiation along soil moisture gradients in tropical moist forests. This mechanism stabilises coexistence of species, because it concentrates species abundance along a part of the soil moisture gradient and thereby increases intraspecific competition relative to interspecific competition. The trade-off in

performance with respect to shade versus drought is also a stabilising mechanism for species coexistence, because it causes species to specialise on coping with either shade or drought, also increasing intraspecific relative to interspecific competition. Thus, water and light availability interactively contribute to the maintenance of species diversity in tropical forests.

I quantified the importance of the soil moisture niche on the demography and distribution of tropical seedlings. Future work may build upon my findings by investigating the morphological, hydraulic or physiological traits that cause the demographic responses to shade and drought in my studies. Additionally, my soil water potential maps can be used to study the effect of water availability on ecosystem functions such as water cycling and carbon sequestration. Finally, my demographic responses to water and light availability can be integrated into Dynamic Global Vegetation Models to better predict the effect of rainfall shifts caused by climate change on the species composition and diversity of tropical forests.

ZUSAMMENFASSUNG

Die Verfügbarkeit von Wasser hat starke Auswirkungen auf die Demografie und Verteilung von Baumarten in tropischen Wäldern. Auf regionaler Ebene bestimmen Unterschiede in Menge und Saisonalität von Niederschlägen die Verteilung der Baumarten. Auf lokaler Ebene ist die Verteilung von Baumarten häufig an topografische oder edaphische Habitate geknüpft, die sich in der Verfügbarkeit von Bodenwasser unterscheiden. Beobachtungsstudien und Experimente in tropischen Wäldern zeigen, dass das Wachstum und die Sterblichkeitsraten von Baumarten durch saisonale und länger andauernde Dürren (z. B. El Niño) beeinflusst werden. Jedoch liegen nur wenige Messungen zur Verfügbarkeit von Bodenwasser in tropischen Wäldern vor. Dadurch ist unser Verständnis darüber, wie Bodenfeuchte einzelne Arten und damit lokale Artenverteilungen, Artenzusammensetzung und Artenvielfalt beeinflusst, stark eingeschränkt. Gleichzeitig ist es weitgehend unbekannt, welche Auswirkungen die Wasserverfügbarkeit in Verbindung mit Lichtverfügbarkeit, einer weiteren stark limitierten Ressource in tropischen Wäldern, auf Baumgemeinschaften hat.

In meiner Dissertation habe ich die Rolle von Bodenfeuchte und Lichtverfügbarkeit auf den Aufbau der Baumgemeinschaft eines tropischen Feuchtwaldes auf Barro Colorado Island (BCI), Panama, untersucht. Dabei habe ich mit meiner Dissertation zwei Hauptziele verfolgt. Das erste Ziel war es, zu bestimmen, wie die Bodenfeuchte die lokal tropischen Baumgemeinschaften in Hinblick auf ihre die Demografie und Verteilung beeinflusst. Das zweite Ziel war es, die Leistung der Baumarten in Bezug auf Wasser und Lichtverfügbarkeit zu bestimmen. Dazu habe ich (1) die räumliche Variation der Bodenfeuchte in einem saisonalen tropischen Feuchtwald quantifiziert, (2) die demografischen Mechanismen bestimmt, durch die Bodenfeuchte die lokalen Baumgemeinschaften prägt, und (3) den Zusammenhang zwischen den Auswirkungen von Wasser- und Lichtverfügbarkeit auf die demografische Entwicklung der Arten untersucht. Diese drei Teilaspekte spiegeln sich in den drei Kapiteln meiner Dissertation wider, während die Ergebnisse übergreifend in der allgemeinen Diskussion behandelt werden.

Meine Arbeit stützt sich auf die Nischentheorie, die postuliert, dass die Trennung von Arten entlang von Ressourcengradienten (i.e. Nischendifferenzierung) maßgeblich zur hohen Artenvielfalt in tropischen Wäldern beiträgt. Ich definiere die Nische als (1) die Leistung und (2) die Verteilung einer Art in Abhängigkeit von Ressourcen (hier: Verfügbarkeit von Wasser und

Licht). Dabei konzentriere ich mich auf realisierte Nischen im Gegensatz zu fundamentalen Nischen, weil ich Arten in ihrer natürlichen Umgebung untersuche, in der sie in Konkurrenz mit anderen Arten stehen. Mein Fokus liegt insbesondere auf der Regenerationsnische, die bei der Demografie und Verteilung von Sämlingen eine besonders wichtige Rolle spielt.

Der erste Schritt meiner Dissertation war die Messung der Verfügbarkeit von Bodenwasser im 50 ha großen Forest Dynamics Plot im saisonalen tropischen Feuchtwald auf BCI; dem ältesten und am besten untersuchten Feuchtwald der permanenten Parzelle im weltweiten CTFS-ForestGEO-Monitoring-Netzwerk. Ich habe die Bodenfeuchte in der regulären Trockenzeit von 2015 und in der schweren Trockenzeit von 2016 gemessen, die mit einer starken El Niño Dürre verbunden war. Ich habe sowohl den Bodenwassergehalt (den Prozentsatz an Wasser im Boden) als auch das Bodenwasserpotential (ein Maß dafür, wie frei sich Wasser im Boden bewegen kann, und so z.B. von Pflanzen aufgenommen werden kann) gemessen. In meiner Arbeit konzentriere ich mich hauptsächlich auf das Bodenwasserpotential (BWP), da es für die Funktion der Pflanzen dahingehend am relevantesten ist, dass Pflanzen das Wasser entlang eines Kontinuums von Boden-Pflanze-Atmosphäre des Wasserpotentials aufnehmen. Insgesamt habe ich 1380 Bodenfeuchteproben an 363 Stellen in der 50-ha-Parzelle genommen, was meinen Datensatz zum detailliertesten Bodenfeuchtedatensatz in einer permanenten Tropenwaldparzelle macht. Ich verwendete diese Daten, um die Bodenfeuchte in der 50-ha-Parzelle (Paper 1) zu kartieren und deren Auswirkungen auf das Wachstum, die Sterblichkeit und die Verteilung von Sämlingen (Paper 2 und 3) zu bestimmen. Diese wurden in 20 jährlichen Zählungen an 200 Sämlingsplots in der Parzelle gemessen.

In Paper 1 quantifizierte ich die räumliche Variation der Bodenwasserverfügbarkeit in der 50-ha-Parzelle auf BCI. Ich habe die BWP für die gesamte Fläche von 50 ha anhand meiner Bodenproben kartiert. Dafür habe ich habe die maschinelle Lernmethode “Random Forest” verwendet, da diese mit dem ungleichmäßigen räumlichen Stichprobendesign rechnen kann. Ich habe in der gesamten Parzelle eine ungleichmäßige Stichprobe genommen, um mögliche Schäden an der Vegetation zu verringern. Um BWP in der Parzelle hinweg zu kartieren, verwendete ich verschiedene räumliche Prädiktoren wie Topographie und Bodentyp. Ich habe auch zeitliche Prädiktoren wie den Zeitpunkt der Probenahme und die Intensität der Trockenzeit zum Zeitpunkt der Probenahme verwendet, welche auf Daten der Bodenfeuchte von einem nahe gelegenen Ort

auf der Insel basierten. Wie erwartet nahm das BWP ab (d. H. Die Böden waren trockener), wenn die Trockenzeit ausgeprägt, die Böden sandig und die Umgebung flach waren. Zusätzlich zu den Karten habe ich R-Code bereitgestellt, den Benutzer anpassen können, um benutzerdefinierte Karten für unterschiedliche Trockenzeitintensitäten zu erstellen. Diese Karten können in zukünftigen Studien zur Artendemografie, -verteilung, -zusammensetzung und -vielfalt sowie zur Funktionsweise des Ökosystems unter aktuellen und zukünftigen Klimabedingungen verwendet werden.

In Paper 2 habe ich den demografischen Mechanismus untersucht, mit dem Bodenfeuchte die Verteilung lokaler Baumarten beeinflusst. Ich hatte erwartet, dass eine erhöhte Sämlingsleistung (Wachstum oder Mortalität) von Arten mit hohem oder niedrigem BWP dazu führen würde, dass ihre Artenverteilungen mit hohem bzw. niedrigem BWP verbunden sind. Ich fand heraus, dass die Wachstumreaktionen auf BWP positiv mit der Artenverteilung zusammenhängen: Arten, die bei höherem (niedrigerem) BWP besser abschnitten, waren abundanter bei höherem (niedrigerem) BWP. Außerdem stellte ich fest, dass Arten, die auf dem feuchten Teil des BWP-Gradienten häufiger sind, an feuchteren Standorten nicht nur schneller wuchsen, sondern auch einen Heimvorteil hatten, d. h, dass sie an feuchteren Standorten schneller wuchsen als Arten die auf dem feuchten Teil des BWP-Gradienten häufiger sind. Die Mortalitätsreaktionen auf BWP standen in keinem Zusammenhang mit der Artenverteilung. Stattdessen nahm die Mortalität mit der Sämlingsgröße stark ab; Größere Sämlinge hatten eine viel geringere Sterblichkeit als kleinere Sämlinge. Ein Wachstumsvorteil in Bezug auf die Bodenfeuchte wirkte sich somit indirekt auf die Artenverteilung aus, indem Arten mit einem Wachstumsvorteil dem verletzlichen Sämlingsstadium schneller entweichen und ihre Sterblichkeit verringern konnten.

Ich fand heraus, dass mehr Arten signifikant eingeschränkte Verteilungen aufwiesen als zufällig erwartet, verglichen mit weit verbreiteten Arten. Dies liefert Hinweise auf Nischendifferenzierung, da die Artenverteilung häufiger auf bestimmte Teile des BWP-Gradienten beschränkt war als auf eine weit verbreitete. Darüber hinaus blieben die Artenverteilungen entlang des BWP-Gradienten über die Lebensphasen von Sämlingen bis hin zu Bäumen konstant, was in früheren Studien, die sich mit topografischen Habitats-assoziationen befassten, nicht festgestellt wurde. Überraschenderweise fand ich relativ wenige signifikante Wachstums- und

Mortalitätsreaktionen auf BWP. Hierfür gibt es mehrere mögliche Gründe. Erstens war der BWP-Gradient aufgrund der relativ flachen Topographie auf BCI relativ flach, was die Unterschiede in der Reaktion der Arten auf BWP einschränkte. Zweitens verhinderte die Ausbreitungsbeschränkung von Arten wahrscheinlich, dass feuchtigkeits-empfindliche Arten ungünstige Stellen erreichen, und schränkte dadurch auch den Bereich der BWP ein, den die Arten erfahren. Drittens hatten viele Arten relativ kleine Stichprobengrößen, was die Unsicherheit in der beobachteten Reaktionen erhöhte. Es gab auch relativ wenige signifikante Habitats-assoziationen zum BWP-Gradienten. Dies war besonders dann der Fall, wenn ich die Artenhäufung und die räumliche Autokorrelation korrigierte, was darauf hinwies, dass die Ausbreitungsbeschränkung die Artenverteilungen beeinflusst, indem Artenhäufungen erzeugt werden, die nicht mit dem BWP-Gradienten assoziiert sind. Zusammengenommen zeigen meine Ergebnisse, dass Variation im BWP Nischendifferenzierung auf BCI bewirkt, wenn auch relativ subtil (d. h. für wenige Arten). Darüber hinaus sind detaillierte Bodenfeuchtemessungen erforderlich, um die Mechanismen zu ermitteln, mit denen die Wasserverfügbarkeit die Artengemeinschaften beeinflusst, da frühere Studien, denen diese Daten fehlten, weder den Zusammenhang zwischen Wachstum und Verbreitung noch übereinstimmende Verteilungsassoziationen zu Habitaten fanden.

In Paper 3 habe ich den Zusammenhang zwischen den Auswirkungen von Wasser und Lichtverfügbarkeit auf die Sämlingsdemografie untersucht. Ich habe das Wachstum und die Sterblichkeit von Sämlingen von Arten auf räumliche Variation in Dürre (d.h. das Gegenteil von der BWP) und zwischenjährliche Variation in Dürre (das maximale kumulative Wasserdefizit, d.h. die Intensität der Trockenzeit) auf Arten, quantifiziert, sowie die räumlich-zeitliche Variation in Schatten (basierend auf dem Vorhandensein oder Fehlen von Vegetation über alle 200 Sämlingszählungsstellen für 20 Jahre). Ich hatte einen Trade-off zwischen den Reaktionen auf Schatten und Dürre erwartet, da ich einen Trade-off bei der Verteilung von Biomasse zwischen oberirdischen und unterirdischen Strukturen erwartete. Ich fand einen Trade-off zwischen den Reaktionen auf Schatten und die zwischenjährliche Variation in Dürre, der darauf hinweist, dass die Fähigkeit von Arten, im Schatten gute Leistungen zu erbringen, auf Kosten ihrer Fähigkeit geht, mit Dürren umzugehen und umgekehrt. Der Trade-off zwischen Reaktionen auf Schatten und Trockenheit ergab sich aus der Abwesenheit von Arten, die sowohl im Schatten als auch bei Trockenheit besonders gut oder schlecht abschnitten. Darüber hinaus wurde der Trade-off

wahrscheinlich durch die Tatsache verstärkt, dass die Lichtverfügbarkeit bei Dürreperioden und an trockeneren Standorten höher ist, so dass schattenempfindliche Arten bei Dürreperioden und dürreempfindliche Arten im Schatten gut abschneiden können.

Überraschenderweise gab es keinen Zusammenhang zwischen Reaktionen auf Schatten und räumliche Variation in Dürre. Das Fehlen eines Zusammenhangs kann auf die relativ schwache Auswirkung der räumlichen Variation in Dürre auf die Leistung zurückzuführen sein. Wie in Paper 2 sind mögliche Gründe dafür der relativ flache BWP-Gradient, die Ausbreitungsbeschränkung und die relativ geringen Probengrößen, die die demografischen Reaktionen der Arten auf BWP begrenzen. Im Gegensatz dazu beeinträchtigten Schatten das Wachstum, und Dürreperioden das Überleben, eines großen Prozentsatzes der Arten. Meine Arbeit legt nahe, dass Schatten und Dürreperioden die Artenleistung stärker beeinflussen als räumliche Schwankungen der Bodenfeuchte. Eine endgültige Aussage über die relative Bedeutung von Schatten und Dürre für die Artenleistung kann jedoch nicht getroffen werden, da die Stichprobengrößen für Schatten und Dürre unterschiedlich waren: Der Schatten wurde nur in der Hälfte der Jahre mit Sämlingszählungen gemessen, was mich daran hinderte, besonders schattenempfindliche Arten in meine Analyse einzubeziehen.

In meiner Dissertation habe ich gezeigt, dass (1) räumliche Unterschiede im BWP am stärksten von Bodentyp und Topographie bestimmt werden, dass (2) Wachstumsreaktionen aufgrund von Wasserverfügbarkeit die Verteilung der Arten auf dem BWP-Gradienten indirekt durch Mortalität beeinflusst und dass (3) es einen Trade-off gibt zwischen demografische Reaktionen auf langanhaltende Dürreperioden (aber nicht räumliche Dürre) und Reaktionen auf Schatten. Ich habe einen neuen Mechanismus aufdecken können, durch den sich erklären lässt, wie räumliche Unterschiede in der Bodenfeuchte die Artenverteilung beeinflussen und dadurch zu Nischendifferenzierungen entlang des Bodenfeuchte-Gradienten in tropischen Feuchtwäldern führen. Dieser Mechanismus trägt zur Erhaltung der Koexistenz von Arten bei, da er die Artenhäufigkeit entlang eines Teils des Bodenfeuchtegradienten konzentriert und dadurch die intraspezifische Konkurrenz im Vergleich zur interspezifischen Konkurrenz erhöht. Der Leistungsverlust in Bezug auf Schatten gegenüber Dürre ist auch ein stabilisierender Mechanismus für die Koexistenz von Arten, da sich die Arten darauf spezialisieren, entweder Schatten oder Dürre zu bewältigen, was auch die intraspezifische Konkurrenz im Vergleich zur interspezifischen

Konkurrenz erhöht und damit auch zur Koexistenz der Arten beiträgt. Wasser- und Lichtverfügbarkeit tragen somit interaktiv zur Erhaltung der Artenvielfalt in tropischen Wäldern bei.

Es ist mir gelungen, die Bedeutung der Bodenfeuchte-Nische für die Demografie und Verbreitung tropischer Sämlinge zu quantifizieren. Zukünftige Arbeiten können auf meinen Erkenntnissen aufbauen, indem sie die morphologischen, hydraulischen oder physiologischen Merkmale untersuchen, die die demografischen Antworten auf Schatten und Dürre in meinen Studien hervorrufen. Außerdem können meine Karten zum Bodenwasserpotential verwendet werden, um die Auswirkungen der Wasserverfügbarkeit auf Ökosystemfunktionen wie den Wasserkreislauf und die Kohlenstoffbindung zu untersuchen. Schließlich können die demografischen Reaktionen auf die Verfügbarkeit von Wasser und Licht in dynamische globale Vegetationsmodelle integriert werden, um die Auswirkungen von Niederschlagsverschiebungen aufgrund des Klimawandels auf die Artenzusammensetzung und die Vielfalt der Tropenwälder besser vorherzusagen.

1. GENERAL INTRODUCTION

The ecological niche (henceforth 'niche') refers to the habitat a species needs for survival and/or a species' role in (or impact on) the community (Chase and Leibold 2003). Separation of species distributions along resource gradients (i.e. niche differentiation) is thought to contribute to the high tree species diversity in tropical forests (Wright 2002). Whereas studies have evaluated the effect of resources (particularly light) on species performance and distributions in tropical forests for decades, little work has been conducted on understanding how differential species performance (growth and survival) with respect to soil water availability may shape tropical tree species communities, likely because high annual rainfall suggested that water availability is not limited in tropical forests. However, large parts of the tropical forest biome consist of seasonal tropical forests with distinct dry seasons (Leigh 2008). In addition, many tropical forests suffer occasional strong droughts, often caused by the El Niño-Southern Oscillation (ENSO) (Phillips et al. 2009, Jimenez et al. 2018). Moreover, shifts in rainfall patterns caused by climate change are expected to influence species composition and ecosystem functioning in tropical forests (IPCC 2014, Allen et al. 2017). Hence, understanding species responses to water availability becomes increasingly important for understanding the diversity and functioning of tropical forests under current and future climate conditions (Corlett 2016).

In this dissertation, I (1) mapped soil moisture across a 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama, (2) determined how the demographic responses (growth and survival) to soil moisture affects species distributions, (3) tested the relationship between demographic species responses to light and water availability. Finally, I discussed the consequences of my findings for species coexistence and identified directions for future studies based on my findings. By taking a demographic approach, I provide a new perspective on the importance of the soil moisture niche for the composition and diversity of tropical forests.

1.1 The niche in this dissertation

The niche concept is used to answer a wide range of questions. For example, niches are quantified as species ranges across climatic gradients to study if climatic niches of invading plant species differ from their native ranges (e.g. Gallagher et al. 2010, Petitpierre et al. 2012). Niches are also quantified in terms of functional traits such as leaf number and shape to determine the overlap in

functional attributes between species (e.g. Mouillot et al. 2005). Several studies have tested the consequences of differentiation of species along niche axes (i.e. niche differentiation) for coexistence (Silvertown 2004), as well as the consequences of complementarity of resource use among species (i.e. niche complementarity) on ecosystem functioning (Loreau 2000). Despite its usefulness, the niche concept is controversial to many ecologists. This is partly because the niche is one of the oldest concepts in ecological thinking, with authors of different scientific eras providing different definitions of the niche. Scientists that use the term niche often do not specify which definition they use, confusing readers. In this section, I introduce different viewpoints on the niche throughout ecological literature and specify my use of the term niche in this dissertation.

The concept of a specific place for each species within the natural world was known to ancient philosophers such as Aristotle as well as to founders of modern ecology such as Linnaeus and Darwin (Pocheville 2015). Grinnell (1917) was the first ecologist to use the word 'niche' in a scientific context, which he saw as all abiotic and biotic conditions that allow a species to exist in a certain place (the 'habitat niche'). In contrast, Elton (1927) focused more on the niche as a position of species in a trophic system (the 'functional niche'). Hutchinson (1957) separated the habitat niche into a 'fundamental' and 'realised' niche, defined as an *n*-dimensional hypervolume of environmental factors in which a species can exist without or with the presence of competitors, respectively. This concept became widely used by researchers to study 'niche theory' when MacArthur and Levins (1967) formalized it as frequency distributions of populations in terms of their resource use (Pocheville 2015).

Niche theory was largely abandoned when it was strongly scrutinized in the 1980s, as various authors showed that many studies did not include adequate null models to test predictions of niche theory (reviewed in Chase and Leibold 2003, Pocheville 2015). In addition, Hubbell (2001) introduced a neutral theory of diversity, which aimed to explain patterns of species composition and diversity without assuming any niche differences among species. In order to make the niche concept useful again in ecological research, Chase and Leibold (2003) redefined the niche as the combined effect from the environment on an organism (i.e. its habitat) and the effect of a species on the community (e.g. through resource depletion). Their definition was based on a mechanistic approach formalised by Tilman (1982), which used population growth of a species

with respect to resource availability and the impact of species on resource availability in a graphical manner to predict the outcome of competition between pairs of species.

I adopt a mechanistic approach to quantifying niches, because I quantify demographic responses to resources (such as soil moisture) as well as their effect on species distributions. Therefore, my definition of the term niche in the dissertation has two components. First, the niche is the demographic response (growth or mortality) of a species to abiotic resources (here: light and soil moisture). Second, it is the resulting distributional association of a species on a resource gradient. Although my definitions of the niche are specific for my dissertation, they are more closely related to the habitat niche than to the functional niche, because I study the responses of species to abiotic conditions and not their roles or functions within the ecosystem. In addition, I focus on Hutchinson's realised niches of species as opposed to fundamental niches, because I work with a naturally regenerating plant community; the effect of competitors on species cannot easily be separated from the effect of resources in an observational study. As I studied seedling dynamics, one can further classify my work as focused on the regeneration niche, i.e. the requirements for an individual to successfully replace a mature individual of the previous generation (cf. Grubb 1977). Finally, I focus on niche differentiation in terms of the current ecological pattern of species' responses to the environment and not on the evolutionary process of species' adaptation to the environment.

1.2 The soil moisture niche in tropical forests

Tree species distributions across the tropics relate strongly to regional rainfall gradients (Baltzer et al. 2008, Esquivel-Muelbert et al. 2017, Amissah et al. 2018). On local scales, species distributions are often related to edaphic or topographic habitats (e.g. Fig. 1) that differ in soil water availability (Harms et al. 2001, Gunatilleke et al. 2006, Chuyong et al. 2011). The abundance of species among these habitats is driven by differences in species performance (Russo et al. 2005, Comita and Engelbrecht 2009, Metz 2012). Drought experiments show that these performance differences and the resulting distributional associations of species to habitats are related to the experimental drought tolerance of species (Engelbrecht et al. 2007a, Comita and Engelbrecht 2009).

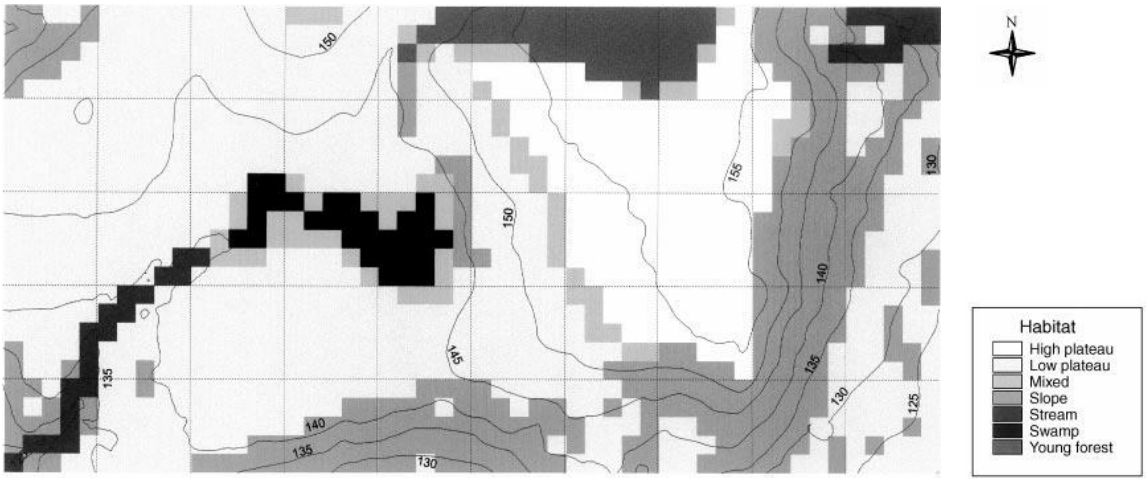

Fig. 1 The 50-ha plot on BCI is classified into seven topographic habitats (Harms et al. 2001).

Separating forest plots in habitats is a good first step for studying the effect of water availability on tree species performance and distributions in tropical forests. However, the use of arbitrary habitat definitions has several disadvantages. First, studies define relatively coarse habitats; generally only three to eight habitats in a 50-ha forest plot (see e.g. Fig. 1, Gunatilleke et al. 2006, Yamada et al. 2010). Thus, habitats allow only for a rough classification of the numerous tree species in these diverse forests. Second, habitats often do not only differ in the availability of soil water but also of nutrients and light (Baltzer et al. 2005, Russo et al. 2012), making it difficult to distinguish between the effects of different resources on tree species communities. Third, habitats are only a proxy for water availability. Few studies on the effect of water availability on tree species performance or distributions measured variation in water availability, and if so they measured soil water content (see e.g. Ashton et al. 1995, De Gouvenain et al. 2007, Uriarte et al. 2018), but see Webb and Peart 2000). However, soil water potential (SWP) best characterises the water availability for plants, as plants extract water from the soil along the soil-plant-atmosphere gradient of water potential (Lambers et al. 2008, McDowell et al. 2008, see Fig. 2). Few studies have measured SWP on a scale that is detailed enough to study its effect on local tree species communities. As a result, the mechanisms by which soil moisture may shape local species distributions in tropical forests remains unclear (McDowell et al. 2018).

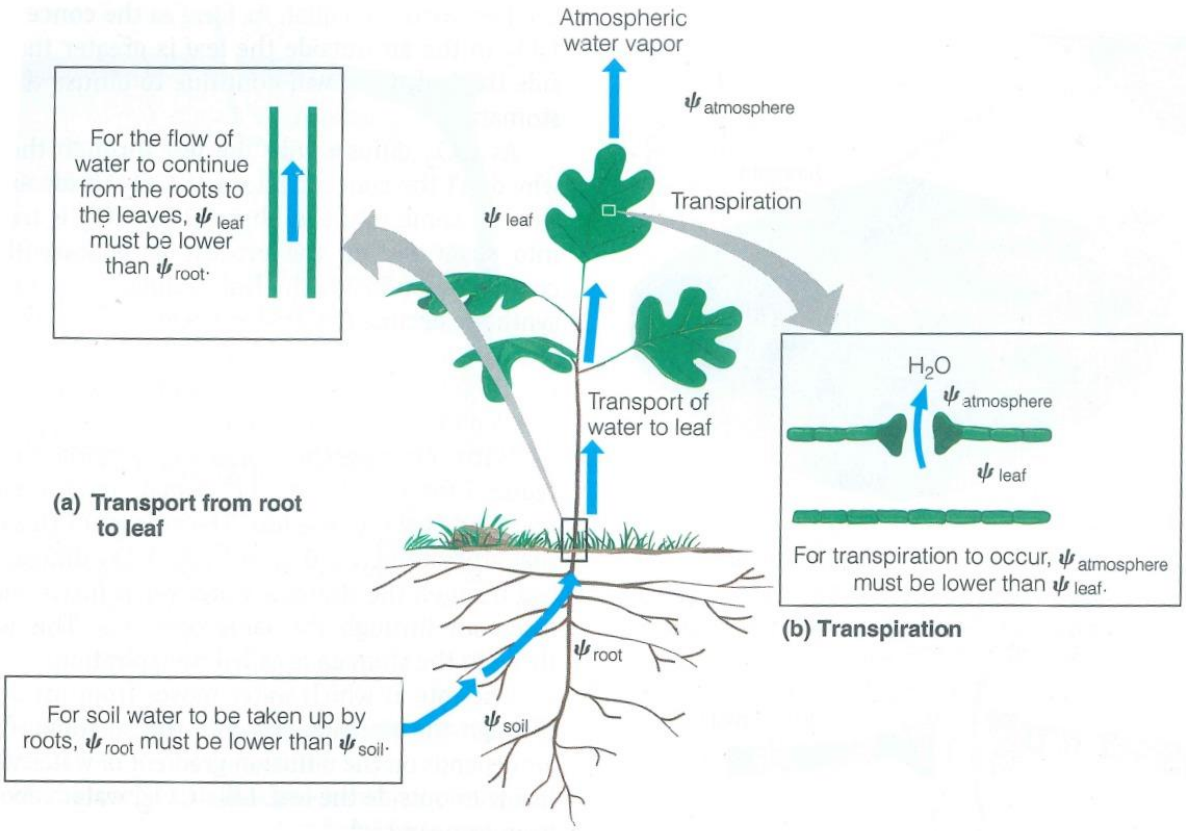

Fig. 2 The decreasing gradient of water potential (ψ) from the soil through the plant to the atmosphere allows plants to take up water from the soil. Figure from Smith and Smith (2006).

I measured SWP across the 50-ha plot on BCI in the regular dry season in 2015 and the severe dry season in 2016, which was related to a strong El Niño drought (see General Methods for details). In Paper 1 of this dissertation (section 3.1), I related SWP to topography (slope and elevation), soil type and other information such as dry season intensity (based on data from a soil moisture monitoring site on BCI). I then mapped soil water potential throughout the 50-ha plot. Based on earlier soil moisture measurements in the plot and in other locations on the island, I expected SWP to decrease with increasing dry season intensity and on flatter terrain (Becker et al. 1988, Daws et al. 2002, Baillie et al. 2007).

In Paper 2 of this dissertation (section 3.2), I studied how seedling demography (growth and mortality) shapes species distributions with respect to SWP. I first determined if there was a community-wide relationship between species distributions along the SWP gradient and how species responded to SWP in terms of growth and mortality. I expected a positive relationship between performance with respect to SWP and species distributions on the SWP gradient, with

species that are more and less drought-sensitive being associated to wetter and drier parts of the SWP gradient, respectively. I expected this because species differ strongly in their drought sensitivity in seedling experiments (Engelbrecht and Kursar 2003). Moreover, experimental drought-sensitivity was related to performance and species abundances in slopes versus plateaus in the 50-ha plot on BCI (Engelbrecht et al. 2007a, Comita and Engelbrecht 2009).

Second, I compared performance of species associated to dry versus wet parts of the SWP gradient. In this way, I could determine if performance differences are strong enough to lead to competitive advantages of one group of species over the other along the SWP gradient. I followed a framework proposed by Fortunel et al. (2016), which proposes that species perform 'best at home' (in my case, on their side of the SWP gradient) as well as have a 'home advantage' (in my case, better performance on their side of the SWP gradient compared to species from the opposite end of the gradient). I expected that drought-sensitive species would perform better under wetter conditions (i.e. 'at home'), whereas drought-tolerant species would be indifferent to SWP (Comita and Engelbrecht 2009). Consequently, I expected that drought-tolerant species would have lower mortality than wet-distributed species on the dry side of the SWP gradient (Brenes-Arguedas et al. 2013). In contrast, I expected wet-distributed species would grow faster on the wet side of the SWP gradient compared to dry-distributed species, because species that originate from wetter forests on the rainfall gradient in Central Panama grow inherently faster than species that originate from drier forests (Brenes-Arguedas et al. 2009, Gaviria et al. 2017).

1.3 The interactive effects of shade and drought on species performance

In addition to water availability, light availability strongly affects plant performance and distributions in many ecosystems (Laanisto and Niinemets 2015). However, the relationship between shade and drought tolerance of species is strongly contested. Smith and Huston (1989) proposed an interspecific trade-off in shade and drought tolerance of plant species regardless of the ecosystem, caused by a trade-off in allocation to belowground structures (roots) to capture water versus aboveground structures (stems and leaves) to capture light. A trade-off in shade versus drought tolerance was found across the northern hemisphere, based on tolerance scores determined from light and water availability of the sites where species occurred as well as on foresters' knowledge (Niinemets and Valladares 2006). When taking species traits such as wood density and seed mass into account, shade and drought tolerance traded off for gymnosperms while

angiosperms exhibited a third strategy of fast growth and stress intolerance (Stahl et al. 2013). Reich (2014) argued that there is a different trade-off between fast growth and low tolerance to shade and drought versus slow growth and high tolerance to shade and drought, based on traits that influence the rate of resource acquisition and growth (e.g. photosynthetic capacity). In that case shade and drought tolerance should be positively related, in contrast to the trade-off hypothesis. A third possibility is that shade and drought tolerance are unrelated, which may be the case when adaptations shade and drought tolerance depend on independent morphological adaptations (e.g. slow growth and high biomass investments in roots, respectively). Independent experimental performance in shade and drought is found in various biomes (Sack 2004, Sánchez-Gómez et al. 2006, Martínez-Tillería et al. 2012).

Shade and drought are particularly challenging for tree species in tropical forests (Grubb 2016). Only around 1% of light reaches the ground in the understory (Chazdon and Fetcher 1984), so variation in light levels caused by treefall gaps provide opportunities for the recruitment of light-demanding species (Augspurger 1984, Poorter 1999). Strong periodic droughts affect species performance in seasonal as well as aseasonal tropics (Corlett 2016). The relationship between shade and drought tolerance in tropical forests may vary within and between dry and moist tropical forests. In tropical dry forests, light demanding species grow fast through high photosynthetic capacity, but this requires high hydraulic efficiency which comes at a cost of hydraulic safety, making them vulnerable to cavitation (Markesteijn et al. 2011). These species are thus shade and drought intolerant and require sites with high light and water availability (Markesteijn et al. 2011). In contrast, evergreen species are more shade tolerant through lower dark respiration, which is coupled with higher hydraulic safety, allowing them to grow in the dark understory and survive drought (Sterck et al. 2011). Thus, shade and drought tolerance are positively correlated in tropical dry forests (Markesteijn et al. 2011, Sterck et al. 2011).

Between dry and moist forest species there is a trade-off in shade and drought tolerance; dry forest species are drought tolerant, i.e. adapted to dry and relatively open conditions compared to moister forests, while moist forest species are more shade tolerant, i.e. adapted to closed and relatively moist conditions compared to drier forests (Poorter and Markesteijn 2008). Within tropical moist and wet forests, soil moisture tends to be lower when vegetation is more open (i.e. in higher light) due to higher evaporation (Marthews et al. 2008, Russo et al. 2012). Similarly,

exposed ridges tend to have lower and more open vegetation and have lower soil moisture than shaded valleys (Ashton et al. 2001, Detto et al. 2013). Additionally, light availability is higher during droughts due to increased solar radiation (Wright and Calderón 2006, Detto et al. 2018). As a result, species would need to cope with either shade or drought, which suggests a trade-off in shade and drought tolerance. However, other studies suggest that gaps have higher soil moisture because there is higher precipitation and there are less tree roots and thus less competition for water (Becker et al. 1988, Veenendaal et al. 1996). Alternatively, moisture may be similar between gaps and understory (Poorter and Hayashida-Oliver 2000). Thus, the relationship between shade and drought tolerance in tropical moist and wet forests remains unclear.

Despite previous work on shade and drought tolerance in the tropics, no study has evaluated the relationship between species performance in shade versus drought under natural conditions within tropical forests. This is largely due to a lack of detailed information on water and light availability. As a result, most studies testing the relationship between shade and drought tolerance in tropical forests have focused on functional traits or species distributions (e.g. Poorter and Markesteijn 2008, Markesteijn and Poorter 2009, Markesteijn et al. 2011). However, whole-plant performance determines population dynamics, which in turn determines species diversity and ecosystem dynamics (McGill et al. 2006). Thus, it remains unclear how shade and drought interact to shape species performance in tropical forests (McDowell et al. 2018).

In Paper 3 of this dissertation (section 3.3), I studied the interspecific relationship between seedling performance (i.e. growth and survival) with respect to shade and drought. I included spatial variation in SWP (i.e. spatial drought), temporal variation in dry season intensity among years (i.e. inter-annual drought) and spatial variation in shade among years (i.e. spatiotemporal shade). I expected a trade-off in species responses to shade and drought. First, I expected that adaptations to cope with shade and drought would trade off (Smith and Huston 1989, Niinemets and Valladares 2006). Trade-offs in traits that allow shade and drought tolerance is certainly not universal (see e.g. Reich 2014), but an experiment with Central Panamanian species showed a trade-off in performance in shade versus drought with several possible trait trade-offs underlying this (Brenes-Arguedas et al. 2013). Second, I expected that shade intensity would be lower during droughts and in drier sites (see above), which would temporarily release shade and drought tolerant species from drought and shade, respectively.

1.4 The role of the soil moisture niche in shaping species coexistence

Species coexistence is maintained by stabilising mechanisms that increase intraspecific competition relative to interspecific competition (Chesson 2000). In Paper 2, I studied spatial niche differentiation along the soil moisture gradient by determining if performance differences among species shape species distributions. If species segregate along the soil moisture gradient as I expected, it would be a stabilising mechanism; species segregation would increase intraspecific competition through increased population densities of species at the part of the soil moisture gradient where they are associated to (Silvertown et al. 2015). In Paper 3, I studied the relationship between demographic species responses to shade and drought. If there is a trade-off between species responses to shade and drought as I expected, it would be a stabilising mechanism as well; species are specialised on one resource and not another, increasing intraspecific competition (Silvertown 2004).

In section 4.4, I evaluate these two stabilising mechanisms (niche differentiation and performance trade-offs) and other mechanisms that may maintain coexistence on BCI, such as negative density dependence (Comita et al. 2014) and niche differentiation with respect to nutrient availability (John et al. 2007). However, I do not draw conclusions on the relative importance of these mechanisms, because I did not quantify their relative importance in this dissertation.

1.5 Outline of this dissertation

The goal of this dissertation was to determine the importance of the demographic and distributional soil moisture niche in shaping the tree species community in the tropical moist forest on Barro Colorado Island (BCI), Panama. To reach this goal, I had two aims. First, I aimed to determine how demographic responses to soil moisture affect species distributions with respect to soil moisture. Second, I aimed to determine the relationship between the demographic responses of species to soil moisture versus light availability.

In Chapter 2 (General Methods) I explain how I measured soil water content and soil water potential (SWP) in the study area, the 50-ha Forest Dynamics Plot on BCI. I also describe other data I used in my dissertation, such as the seedling census and light availability data. Finally, I explain my modelling approaches to map soil moisture across the 50-ha plot and to quantify species responses to soil moisture and light availability.

In Chapter 3 (Original Contributions) I present the papers that allow me to reach the aims of the thesis (Fig. 3). In Paper 1, I used my measurements to map soil water availability across the plot at various stages of the dry season. In Paper 2, I studied the demographic responses of species to SWP in terms of seedling growth and mortality. To determine whether the demographic responses to SWP affected the realised niche of the species (my first aim), I related the responses to the distributional centre of the species along the SWP gradient. In Paper 3, I studied seedling growth and survival responses to soil water potential and light availability. I then tested if there was a relationship (e.g. a trade-off) between species responses to soil moisture versus light availability (my second aim).

Finally, I discuss my findings in Chapter 4 (General Discussion) to reach the goal of my dissertation. I evaluate how my work deepens our understanding of the role that soil moisture plays in the performance and distribution of tropical forest tree species, as well as its implications for species coexistence (Fig. 3). I discuss how the results of this dissertation can be used in future research, for example for studying the effect of water availability on ecosystem functioning of tropical forests and for predicting how changes in water availability due to climate change may alter future species composition and diversity in tropical forests.

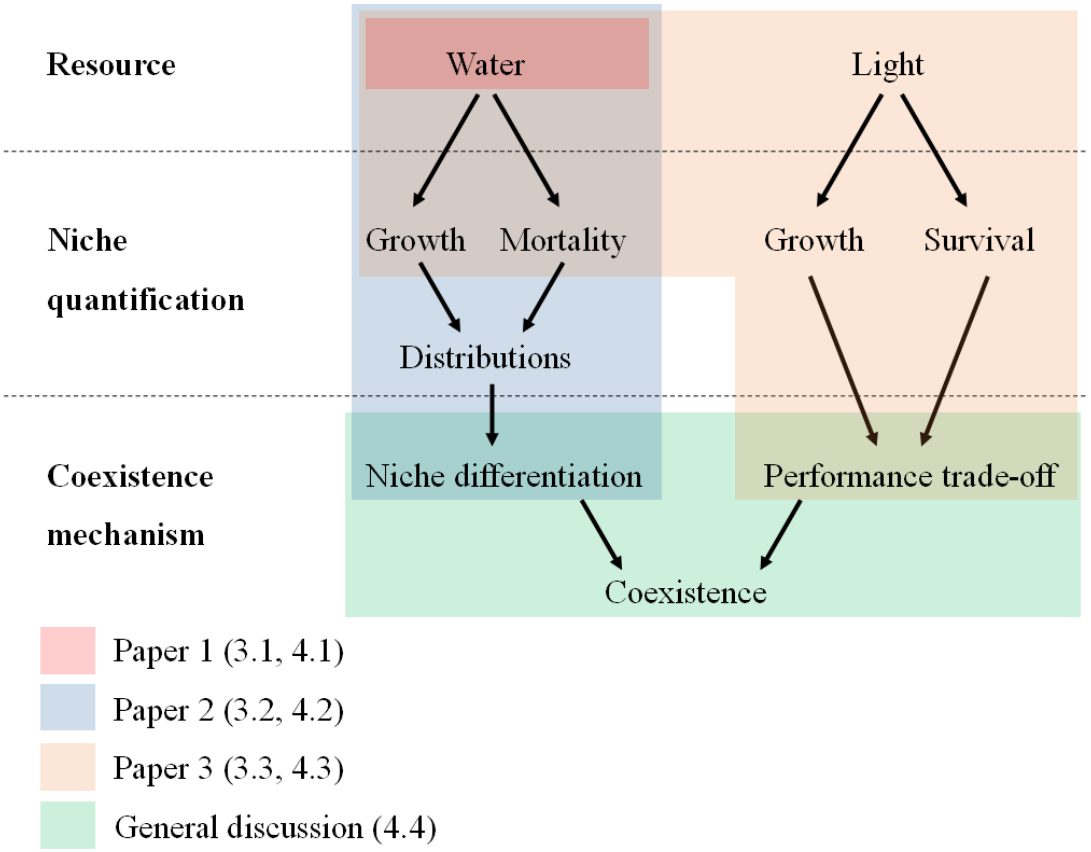

Fig. 3 Conceptual overview of the three papers of my dissertation (sections 3.1-3.3) and the structure of the discussion (section 4.1-4.4).

2. GENERAL METHODS

In this chapter I provide an overview of the methods used in this dissertation. A detailed description of the methods for each paper is given in sections 3.1-3.3. All data produced for this dissertation are freely available through Dryad and Figshare (Kupers et al. 2018, Kupers et al. 2019) and through the iDiv Data Repository (http://idata.idiv.de/ddm/Data/ShowData/287). All analyses were conducted in R version 3.4.1 (R Core Team 2017).

2.1 The 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama

Barro Colorado Island (BCI) is located in the Gatun Lake in Central Panama (Fig. 4). BCI is a former hilltop which became an island through the creation of the Panama Canal in 1914 (https://stri.si.edu/facility/barro-colorado). The island has been a reserve since 1923 (Leigh 1999). It lies halfway of a rainfall gradient spanning from the dry forest of the Pacific shore to the rainforest of the Caribbean shore (Leigh 1999). Rainfall averages 2660 mm per year and is highly seasonal, with only 10% of the rain falling in the dry season from mid-December until late April (STRI 2019). Except for a few clearings the island is completely forested with semi-deciduous moist tropical forest (Croat 1978).

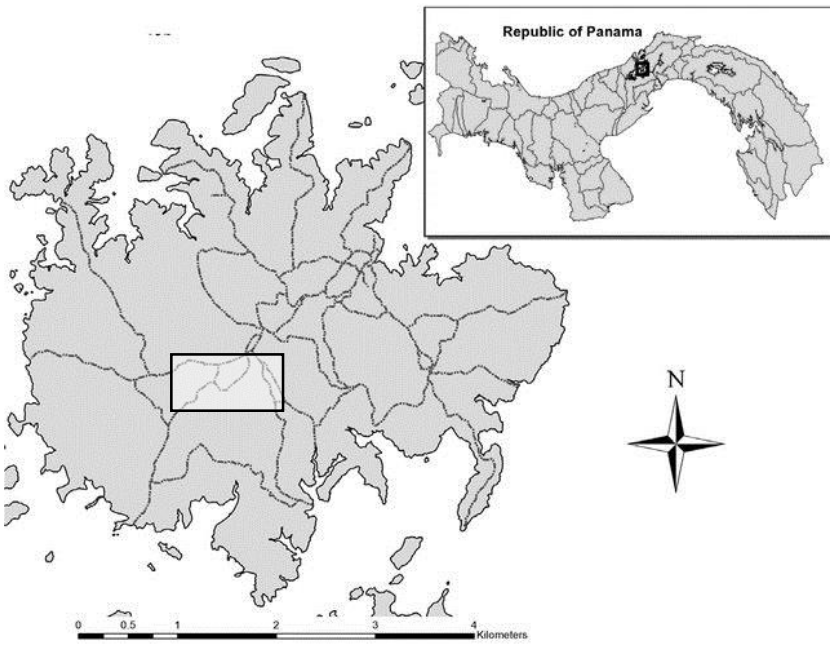

Fig. 4 Barro Colorado Island is located in Gatun Lake in Central Panama. The shaded rectangle in the centre of the island indicates the 50-ha Forest Dynamics Plot (adapted from Rodgers et al. 2015)

The 50-ha Forest Dynamics Plot was established by the Smithsonian Tropical Research Institute (STRI) in 1980 (Hubbell and Foster 1983). It was the first plot established in the Center for Tropical Forest Science (CTFS) – Forest Global Earth Observatory (ForestGEO) network of permanent forest research plots around the world (Anderson-Teixeira et al. 2015). The plot is one of the best-studied tropical forests in the world (Leigh 2008). Most of the plot consists of old growth forest (> 200 years old), except for 2 ha that is in late secondary succession (> 100 years old) (Hubbell and Foster 1983, Foster and Brokaw 1996). The plot lies on a relatively flat plateau, with elevation ranging from 120 to 155 m a.s.l (Hubbell and Foster 1983). It has been classified into seven topographic habitats to facilitate studies on species performance and distributions in the plot (see Fig. 1 and section 1.2).

Other studies have measured several plant resources and abiotic conditions in the plot. Soil water availability was measured at four locations in the 50-ha plot, which showed that gaps were wetter than the understory and that slopes were wetter than plateaus (Becker et al. 1988). Annual canopy censuses have been conducted on a 5 m grid throughout the plot during 12 years to estimate vegetation density (Condit 2019). These censuses have been used to estimate light availability across the plot (Rüger et al. 2009). I used these data on light in my dissertation to compare the effect of light on plant performance with the influence of water availability which I measured in the plot (see section 2.3). Various nutrients and soil chemistry variables (such as pH and cation exchange capacity) have been measured on a 28m grid in the plot (Wolf et al. 2015). I used these data in Paper 2 to evaluate correlations of soil chemistry and my water availability measurements to determine possible influences of soil chemistry on my estimates of demographic species responses to water availability (see section 3.2).

2.2 Vegetation censuses

I analysed seedling growth and mortality Paper 2 and 3 (section 3.2 and 3.3). Seedlings were censused annually from 1994 to 2014 at 200 seed trap sites located at 4-10 meters along the trails of the plot (Wright et al. 2005). Each seed trap has three 1-m^2 seedling census plots surrounding it (Fig. 5). The seed traps cover all topographic habitats of the 50-ha plot except streamsides (cf. Harms et al. 2001). Every dry season, seedlings of woody species in the seedling plots are identified to species, their heights are measured and mortality is recorded (Wright et al. 2005). Another seedling census was established in 2001 (Comita et al. 2007a). Similar 1-m^2 seedling plots

were established in each 5x5m subquadrat of the 50-ha plot, totalling 20 000 plots. Only seedlings ≥ 20 cm height were measured, and plots were censused annually except for 2005, 2007 and 2010. I used data from this network of plots in Paper 2 to compare seedling distributions with respect to water availability. Every five years, growth and status (dead/alive) of all trees ≥ 10 cm dbh is recorded and new recruits are identified to species, tagged and measured (Condit 1998). I used data from these censuses in Paper 1 and 2 (section 3.1 and 3.2, respectively), where I calculated basal area as a predictor of soil moisture throughout the 50-ha plot (Paper 1) and compared distributions of trees with respect to soil moisture with those of seedlings (Paper 2).

a) b)

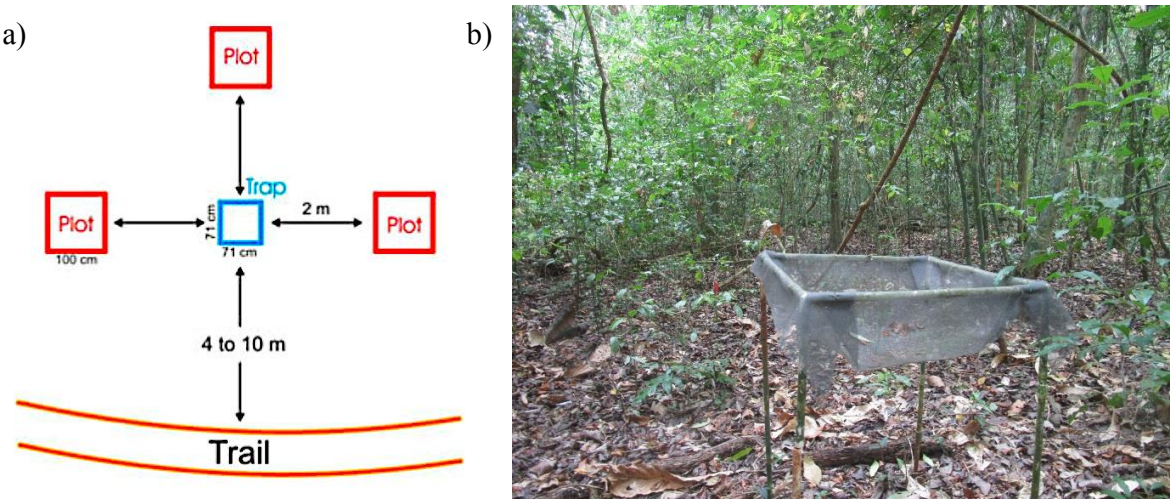

Fig. 5 The trails in the BCI 50-ha plot are flanked by 200 seed traps (see also Fig. 6). a) Each seed trap is surrounded by three seedling census plots, located 2 meters from the trap (ForestGEO 2018). b) Seedling plots are marked with a coloured flag around 30 cm from the forest floor, here visible in pink just left from the elevated seed trap structure (Photo: Stefan Kupers).

2.3 Soil moisture sampling

I conducted a soil moisture sampling campaign in the 50-ha plot during the dry seasons of 2015 and 2016. Together with teams of five assistants I took samples during three periods in the 2015 dry season (February, March and April) and one period in the 2016 dry season (March). The dry season in 2016 was associated with the 2015-2016 El Niño, and was the third longest dry season on the island since 1954 (STRI 2017). In total, we took samples at 363 sites, consisting of the 200 seed trap locations along the trails of the 50-ha plot and 163 other sites in the plot and around its perimeter (Fig. 6). In all four sampling periods we took samples at the seed traps because they

were easily accessible, limiting disturbance to the vegetation in the plot. I used these data in Paper 2 and 3 to study the effect of soil moisture on seedling demography and distributions (sections 3.2-3.3). In April 2015 and March 2016 we took samples until 40 cm depth at 100 sites along five north-south transects, as well as 41 sites targeting steep slopes (> 15°), rare habitats such as treefall gaps, the swamp and streamsides. We also took samples until 100 cm depth at 22 sites around the borders of the plot during the three sampling periods in 2015. I used data from all sampling locations in Paper 1 to map soil moisture across the 50-ha plot (section 3.1). Finally, I assessed small-scale variation in soil moisture at eight seed trap locations by taking samples at different distances from the trap (Paper 1).

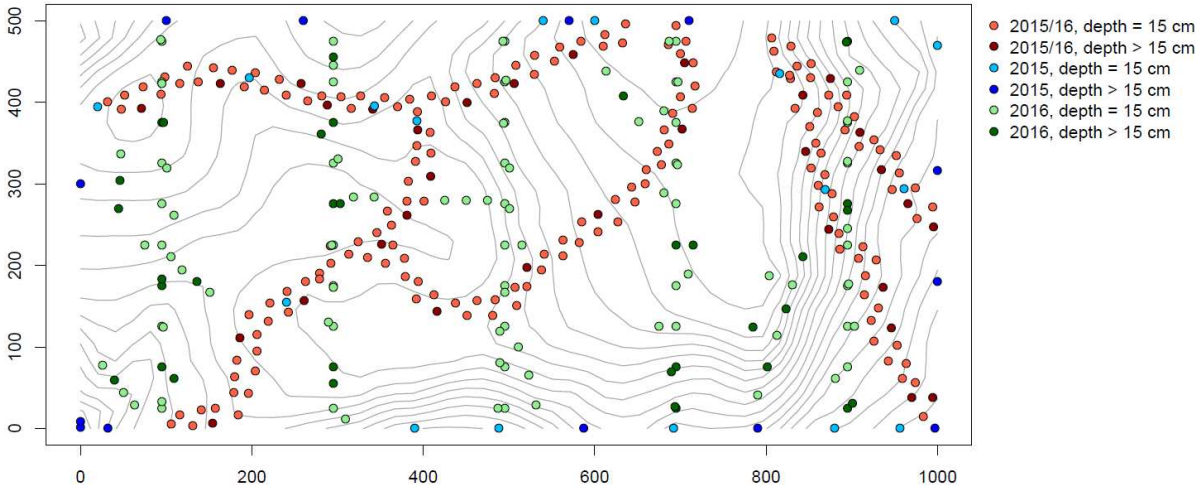

Fig. 6 Sampling locations and the depth of sampling in the 50-ha plot (published in Paper 1). Samples at 15 cm depth were taken at all sampling locations. Samples deeper than 15 cm were taken until 40 cm in the plot and until 100 cm around the plot perimeter.

We took soil samples with 1-3 cm diameter augers depending on the depth of the soil (Fig. 7). We inserted the auger until the depth mentioned above. The bottom 1 cm of the core was sealed in airtight plastic vials for soil water potential measurements and zip lock bags for soil water content measurements. We transported the soils to the laboratory in isolating containers with cooling elements. We measured soil water potential (SWP) of each vial sample within a day after collection with a WP4C Dewpoint PotentiaMeter (Fig. 8). Soil water potential is the relevant measure of water availability for plants, because plants draw water from the soil along a soil-plant-atmosphere continuum of water potential (Lambers et al. 2008). We also assessed gravimetric soil

water content (SWC) for each bagged sample from fresh mass (f) and dry mass (d) determined after 72 hours in a drying oven at 105°C (SWC = (f–d)/d) (Fig. 9). I used these data to compare temporal variation in SWC in the 50-ha plot with SWC monitored in the Lutz Catchment, 1.25 km from the 50-ha plot (see Paper 1 and 2). Finally, we reused a subset of the vial samples to measure soil water retention curves, which represent the relationship between soil water potential and soil water content for a particular soil type. I used these curves to determine outliers in soil water potential (see Paper 2 and 3).

a)  b) 

Fig. 7 a) Gauge augers with cylindrical chambers were used for obtaining soil samples with undisturbed texture. b) In rare cases, soils at different depths varied markedly in colour (Photos: Stefan Kupers and Darina Iskreva).

Fig. 8 We used the WP4C DewPoint Potentiameter (Decagon Devices, Inc., Pullman WA, USA) to measure soil water potential (SWP) of all our soil samples. The WP4C provides precise SWP measurements with an accuracy of 0.05 MPa (Decagon Devices 2010).

Fig. 9 Soil samples after drying for 72 hours in a drying oven. These dried samples show the variation in soil texture and colour of soils in the 50-ha plot (Photo: Stefan Kupers).

2.4 Mapping soil water potential with Random Forest

In Paper 1, I used the soil moisture sampling data to map soil water potential (SWP) throughout the 50-ha plot. My soil sampling sites were mostly concentrated at seed traps along the trails to prevent disturbance to the vegetation in the plot (see Fig. 6), which prevented me from using common mapping approaches such as interpolation (Brus 2019). Instead, I applied a machine learning algorithm called Random Forest (Breiman 2001). Random Forest was best suited for the spatial distribution of my soil moisture samples, because can handle spatial data that is unevenly sampled (Li et al. 2011). Random Forest is an ensemble method, i.e. it creates various individual models that are averaged to get a final prediction, which increases predictive performance compared to single models such as multiple regression (Dietterich 2000, Liaw and Wiener 2002).

I used Random Forest to predict spatial variation in SWP from various data sources such as topography, soil type and tree basal area as predictors (see Paper 1). Random Forest creates many independent decision trees (see Fig. 10). Decision trees use binary splits to predict a response variable from a bootstrapped sample of the data using a random subset of predictor variables (Liaw and Wiener 2002). The decision trees are aggregated, taking the mean of the predicted value of each observation as predicted from the single trees (Fig. 11, Breiman 2001). Finally, I used the spatial information from each grid cell (e.g. elevation, slope and soil type) and fixed the value of temporal variables (e.g. dry season intensity and time of the day) to map SWP throughout the 50-ha plot. I present maps of several stages of dry season severity in paper 1. Additionally, I provide code that users can adapt to create maps of any date in the dry season to facilitate various research projects.

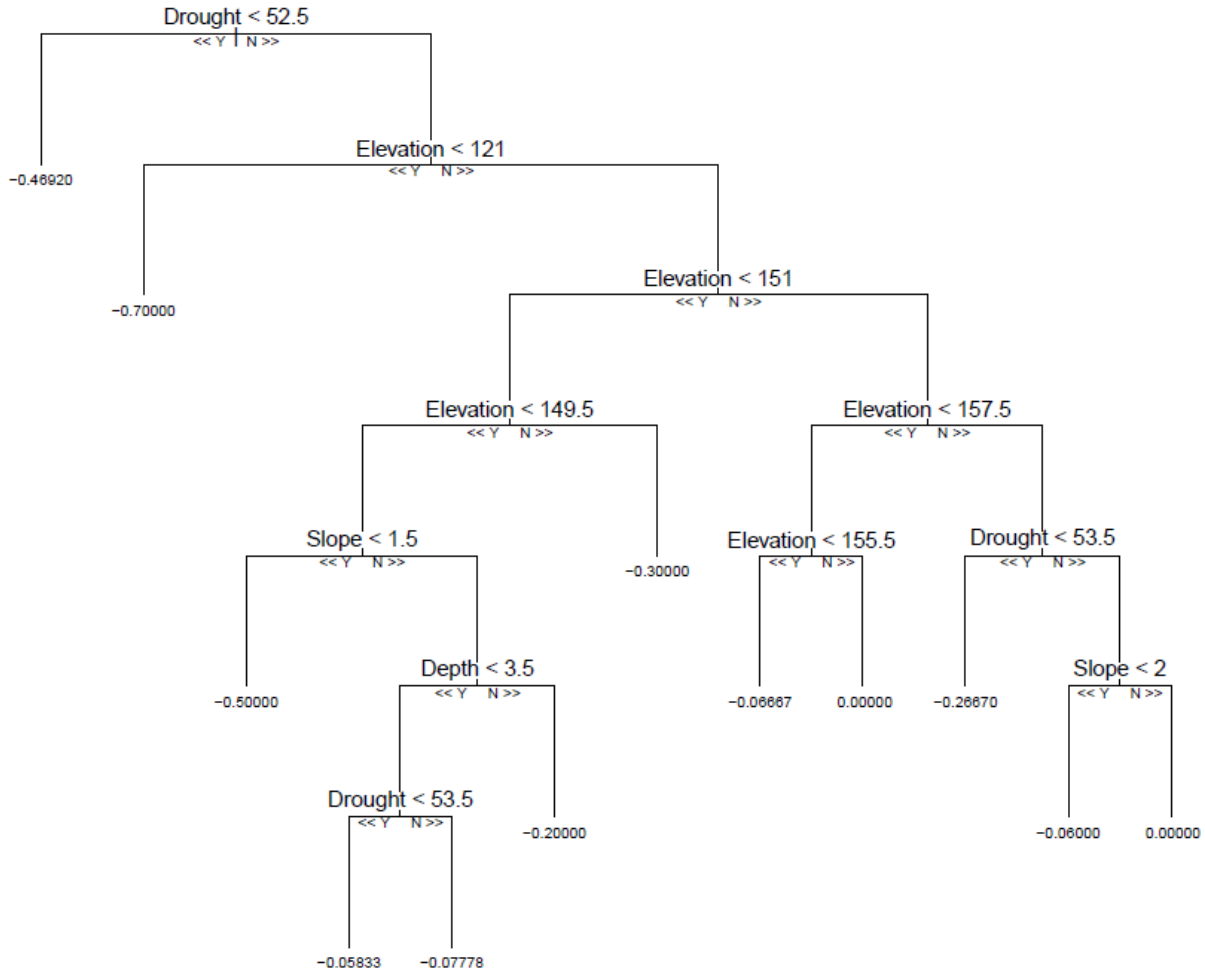

Fig. 10 Example of a decision tree that is part of a Random Forest model predicting soil water potential (SWP). To predict SWP, an observation follows the tree from the top based on binary splits, following Y if the statement is true and N if it is false, and descends until it reaches the end of a branch (i.e. a terminal node). Values below the terminal nodes indicate predicted SWP values (MPa) of observations belonging to that node. In the final Random Forest model, I averaged SWP predictions of 1000 decision trees. For readability, SWP in this tree is only predicted from elevation (m), slope (°) and drought (i.e. dry season severity quantified as soil water content (%) monitored 1.25 km from the 50-ha plot). All predictors are given in Paper 1.

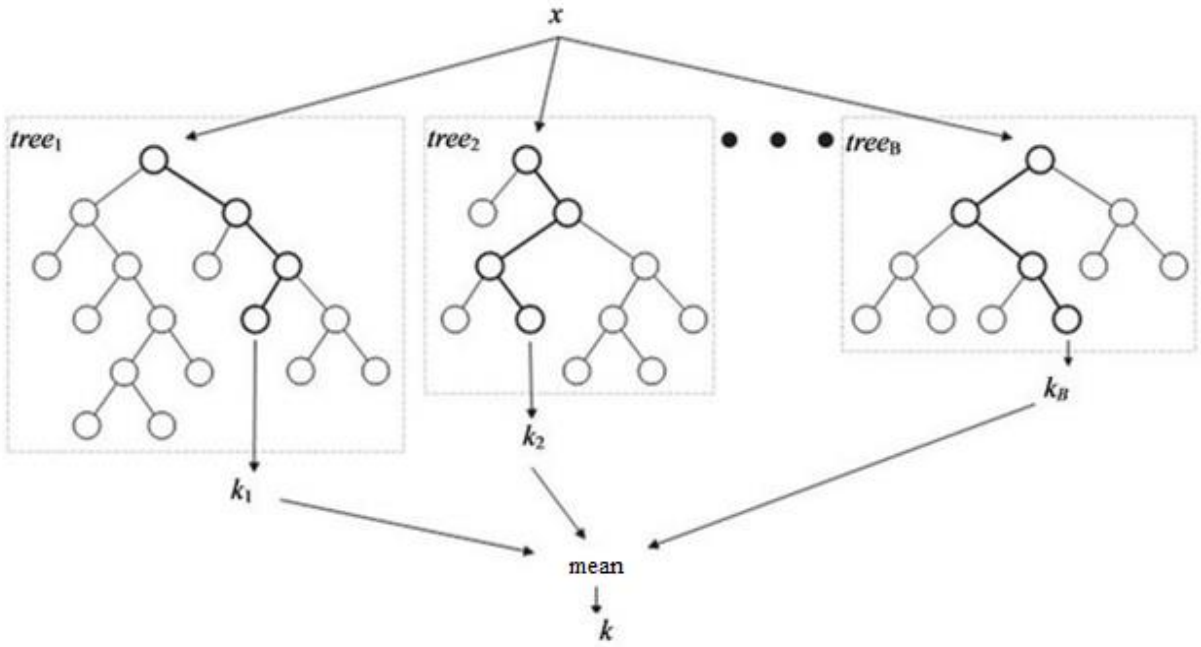

Fig. 11 Schematic representation of a Random Forest model. *B* decision trees are created first (see Fig. 10). An observation *x* follows each decision tree to the end (a terminal node) and gets a predicted value (k_B). The predicted values are then averaged to determine the final predicted value *k*. Figure adapted from Zhang et al. (2018).

2.5 Quantifying the effect of soil moisture on seedling demography using Hierarchical Bayesian modelling

In Paper 2 and 3, I studied the effect of soil moisture and light availability on seedling demography (growth and mortality) and local distributions in the 50-ha plot. I directly used the soil moisture data collected at the seed traps, because the seedling plots were located next to the soil sampling sites (see Fig. 5). In both papers, I used a hierarchical Bayesian approach to estimate the growth and survival responses as well as the link between demographic responses and species distributions.

Bayesian statistics are an alternative to frequentist (or 'classical) statistics (Clark 2005). The debate on the philosophical difference between Bayesian and frequentist statistics date back at least 250 years and has been particularly strong since the 1960s (Clark 2005, Efron 2005). In short, frequentist statistics assume that there is a 'true' value of the parameter that they are estimating with their model, while Bayesian statistics view parameters as values that vary within

a probability distribution (Ellison 2004, Clark 2005). Additionally, Bayesian statistics use prior knowledge together with sampled data while frequentist statistics use only sampled data (Ellison 2004). I refer to Efron (2005) for an overview of the philosophical and conceptual differences between Bayesian and frequentist statistics, while I focus here on the practical differences. In practice, frequentist statistics focus on hypothesis testing (e.g. using *p*-values), while Bayesian statistics tend to focus on quantifying probability distributions of parameters (Wagenmakers et al. 2008). In a Bayesian model framework, uncertainty in each parameter estimate can be explicitly modelled and analysed (Ellison 2004, Clark 2005). This was advantageous for my work, because it allowed me to correctly quantify uncertainty in the response of individual species to soil moisture and light availability. Additionally, the Bayesian framework enables the formulation of hyperdistributions, which are overarching parameter distributions that quantify e.g. means and standard deviations of a group of parameters (Clark 2005). This allowed me to account realistically for variation in e.g. growth or mortality differences among individuals or years (Clark 2005). Finally, the hierarchical structure allowed relatively rare species to contribute information to the model while being correctly weighted by their abundance (Rüger et al. 2011b).

A hierarchical Bayesian approach dissects complex modelling problems into levels (Clark 2005). Fig. 12 shows the four levels of the growth model from Paper 2. Growth data of seedlings (*obs*) enter the model in the data layer. Observed growth varies around predicted growth (*pred*) with a lognormal distribution. In the process level, growth is predicted from soil water potential (*SWP*) and seedling height (*H*), with random effects for individual (u_i), seedling census site (u_s) and year (u_y). The parameters feed into the equation predicting growth in the data layer, and the parameter quantifying responses of species to SWP (β_1) also feed into the equation that links SWP responses to observed species distributions *D* in the process layer. Various parameters depend on means (μ) and standard deviations (σ) of parameters across the community from the hyperparameters layer. A detailed description of the models can be found in Paper 2 and 3.

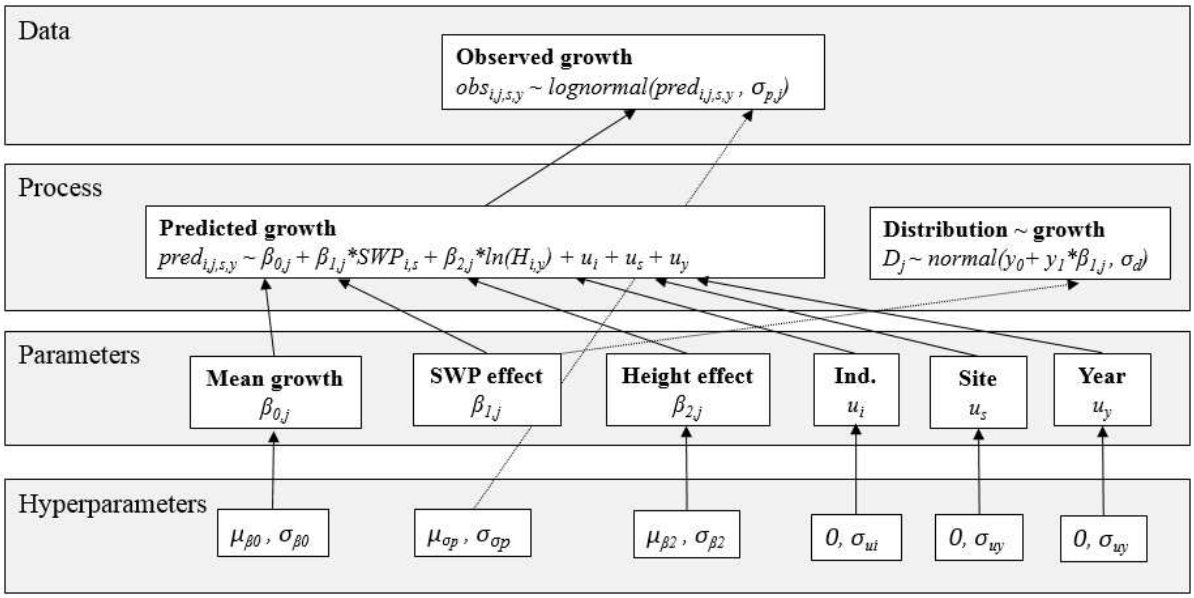

Fig. 12 Graphical representation of the hierarchical Bayesian growth model in Paper 2. Figure adapted from Rüger et al. (2009).

In Bayesian models, estimating probability distributions of parameters requires sampling from a proposed distribution using a Markov Chain Monte Carlo (MCMC) algorithm (for details see Hobbs and Hooten 2015). Many iterations (typically 1,000 to 10,000) are needed to provide reliable distributions of parameters (Hobbs and Hooten 2015). As a result, running hierarchical Bayesian models requires high computing power (Clark 2005), even though several MCMC chains can be run in parallel. I wrote and tested my Bayesian models in R using the package RStan (Stan Development Team 2017). I tested if parameter estimates were accurate by comparing SWP and height responses of a few common species with parameter estimates from frequentist methods such as linear regressions fitted separately for these species. Additionally, I tested if models converged by inspecting diagnostic plots such as trace plots that visualise MCMC sampling and diagnostic values such as the potential scale reduction factor (*Rhat*) that indicate the potential reduction in the width of parameter confidence intervals if MCMC sampling is continued (Gelman and Hill 2007). I typically ran various test models at the same time on a High Performance Cluster managed jointly by UFZ and iDiv in Leipzig. When a tested model gave realistic parameter estimates and converged rapidly, I ran full models with 10,000 iterations, which I presented in Paper 2 and 3.

3. ORIGINAL CONTRIBUTIONS

3.1 Paper 1: Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama

Kupers, S.J., Wirth C., Engelbrecht, B.M.J., Rüger, N. Scientific Data 6 (63):1–9 (2019). https://doi.org/10.1038/s41597-019-0072-z

SCIENTIFIC DATA

OPEN

DATA DESCRIPTOR

Received: 21 January 2019
Accepted: 12 April 2019
Published online: 17 May 2019

Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama

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Fine scale spatial variation in soil moisture influences plant performance, species distributions and diversity. However, detailed information on local soil moisture variation is scarce, particularly in species-rich tropical forests. We measured soil water potential and soil water content in the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama, one of the best-studied tropical forests in the world. We present maps of soil water potential for several dry season stages during a regular year and during an El Niño drought. Additionally, we provide code that allows users to create maps for specific dates. The maps can be combined with other freely available datasets such as long-term vegetation censuses (ranging from seeds to adult trees), data on other resources (e.g. light and nutrients) and remote sensing data (e.g. LiDAR and imaging spectroscopy). Users can study questions in various disciplines such as population and community ecology, plant physiology and hydrology under current and future climate conditions.

Background & Summary

Water is an essential resource for plants and is crucial for numerous plant functions[1]. Consequently, water availability strongly influences plant performance, species distributions, functional composition and ecosystem functioning across biomes[2–6]. On local scales, spatial variation in soil moisture differentially affects performance among species[7–9], promoting niche differentiation in plant communities and fostering coexistence[10]. Understanding how local soil moisture variation affects plants will become increasingly important, given the predicted shifts in rainfall patterns caused by climate change and their expected effects on plant performance, community composition and species distributions[2,4,11].

In tropical forests, local variation in soil moisture causes tree species to perform differently among habitats[12–14], which promotes habitat associations and may contribute to the maintenance of high species diversity in these forests[8,15,16]. However, soil moisture also affects species performance and distributions at smaller scales than habitats, highlighting the importance of measuring fine-scale spatial variation in soil moisture[9]. Most studies that link species performance to soil moisture have measured soil water content[17–20]. Yet, soils with similar water contents can differ in characteristics that influence the availability of water for plants, such as texture, bulk density and pore size distribution[21,22]. A more relevant measure for plant-water relations is soil water potential, because plants extract water from the soil along a soil-plant-air gradient of water potential[23].

We measured dry-season soil water potential and soil water content across a 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama (Fig. 1). The plot consists of seasonal lowland tropical forest, a forest type that occurs in large parts of the tropical regions of Africa, Asia and Latin America[24]. The 50-ha plot was established in 1981 and is the first plot in the global CTFS-ForestGEO network[25,26]. Regular censuses document the entire

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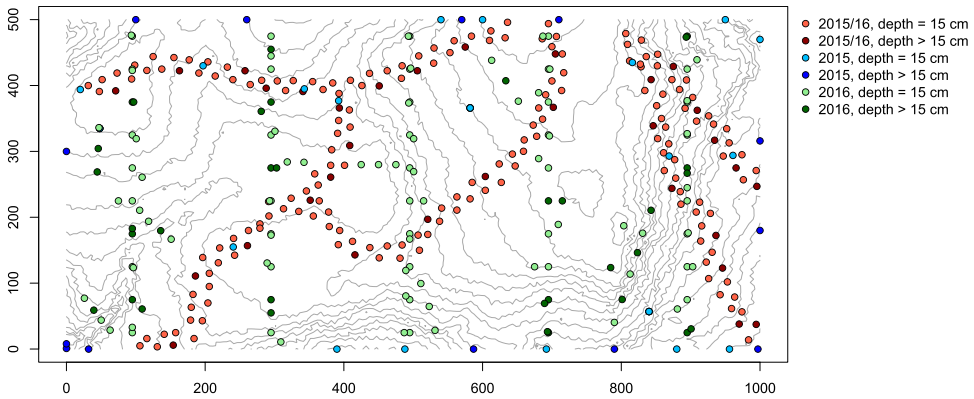

Fig. 1 Sampling locations and depth of soil sampling in the 50-ha plot on BCI, Panama, during the dry seasons of 2015 and 2016. Samples >15 cm depth within the 50-ha plot and around the plot perimeter were taken down to a depth of 40 cm and 100 cm, respectively. Intervals of the contour lines are 2 m.

Variable	Type	Source
Elevation	Spatial (horizontal)	ForestGEO[46]
Slope	Spatial (horizontal)	ForestGEO[46]
Soil type	Spatial (horizontal)	Baillie *et al.*[44] and Harms *et al.*[43]
ln(Basal area) of trees ≥1 cm dbh in the 2015 census	Spatial (horizontal)	Hubbell *et al.*[36]
ln(Depth) of soil sampling	Spatial (vertical)	Soil sampling records[52]
Time of soil sampling	Temporal	Soil sampling records[52]
Monitored soil water content	Temporal	Smithsonian Tropical Research Institute[47]

Table 1. Variables used in the Random Forest models.

life cycle from seeds to adults for more than 300 species of trees and climbers, making it one of the best-studied tropical forests in the world[24,26–28]. Because of the strong seasonality and inter-annual variation in rainfall and soil moisture on BCI, we measured soil moisture across several stages of a normal dry season and a dry season associated with a severe El Niño drought[29]. We used Random Forests[30] to model spatial variation in soil water potential across the 50-ha plot on a 5 m resolution during various stages of the dry season, using soil monitoring data to quantify drought intensity, as well as topographic and edaphic information and data from a tree census (see Table 1). We provide the original soil moisture data and adjustable code that allows users to create custom maps for any date in the dry season since 1975 and to apply different model settings or algorithms.

The approach we developed generates soil water potential maps at very high spatial and temporal resolution (i.e. 5 m resolution for any day). These data, therefore, are ideal for studies that focus on ecological or hydrological processes on a local scale[1,31]. In addition, they complement soil moisture estimates from satellite data, which are ideal for upscaling local measurements to regional scales (e.g., across a climatic gradient). Recently launched satellites such as Sentinel 1 and 2 have the potential of estimating soil water content on a maximum resolution of 100 m[32,33]. In the future, these high-resolution soil moisture products from Sentinels can be compared with our *in-situ* measurements.

The maps can be combined with various datasets collected in the 50-ha plot, such as surveys of light availability[34] and soil chemistry[35], long-term censuses of flowers, seeds and seedlings[28] and trees[36], and detailed remote sensing datasets such as airborne imaging spectroscopy[37] and light detection and ranging (LiDAR) data[38]. Users may explore the role of soil moisture in various fields of research such as community assembly, niche differentiation and coexistence, hydrology and nutrient transport, and soil carbon cycling and storage. In addition, the maps of various dry season conditions can be used to plan new observational studies, to quantify the effect of climate variability (such as El Niño droughts) on the performance and distribution of tree species and to predict the effect of expected shifts in rainfall patterns caused by climate change[11].

Methods

Study site. The 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama (9.15°N, 79.85°W), supports semideciduous lowland moist tropical forest[39]. Most of the plot is old growth forest (>300 years old), except for 2 ha that is in late secondary succession (>100 years old)[26]. Rainfall is strongly seasonal: only 10% of the 2660 mm annual precipitation falls in the dry season from mid-December to late April[29]. The intensity and length of the dry season are highly variable, and dry seasons during El Niño events tend to be particularly long[40].

The topography of the 50-ha plot is relatively flat with slopes ranging from 0 to 21 degrees, and elevation ranging from 120 to 155 meters asl[26]. Soil water availability is higher (i.e. soil water potential is less negative) on

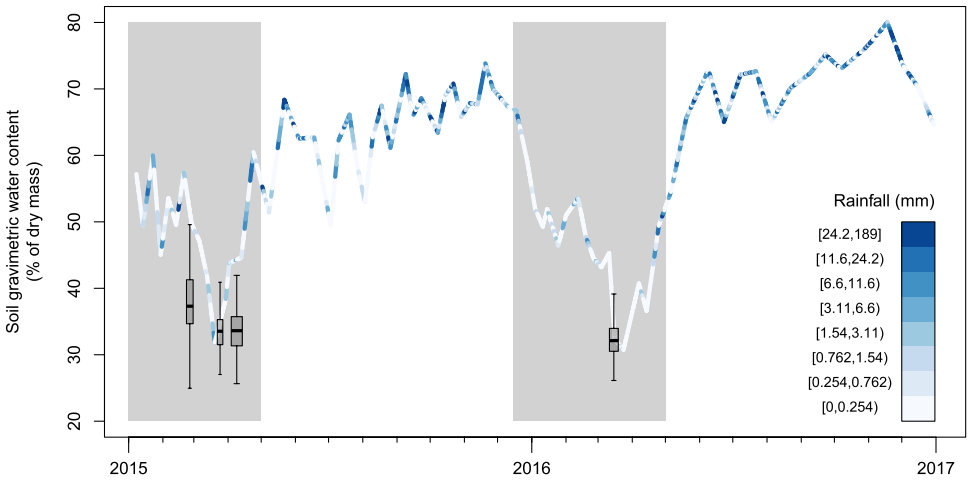

Fig. 2 Soil water content (SWC) measured in the 50-ha plot in the four sampling periods (box and whisker plots) and monitored 1.25 km from the 50-ha plot (lines). The width of the boxes represents the number of days in the sampling period (see Methods). Colours indicate daily rainfall. Grey shading indicates dry seasons. Rainfall and SWC monitoring data are from the Smithsonian Tropical Research Institute (STRI) Physical Monitoring Program[47].

		# of samples	% of samples	% of plot area
Habitat	High plateau	93	7.2%	13.6%
	Low plateau	669	51.5%	49.6%
	Mixed	55	4.2%	5.3%
	Slope	292	22.5%	22.7%
	Stream	46	3.5%	2.6%
	Swamp	25	1.9%	2.4%
	Young	119	9.2%	3.8%
Soil type	AVA	796	61.2%	71.9%
	Fairchild	46	3.5%	0.8%
	Marron	429	33.0%	25.0%
	Swamp	28	2.2%	2.3%

Table 2. Number and percentage of samples taken in each habitat and soil type, and the percentage of the plot area covered by each habitat and soil type.

slopes than on plateaus[41,42] due to the geology and hydrology of the plot; the water table is close to the surface and creates several springs on the slopes, and water drains via the slopes that form the edges of an andesite cap with low permeability underlying the high plateau[39,41,43]. There are four types of red clay soils defined in the local soil classification system for BCI: AVA covers most of the flat terrain across the plot, Marron covers the eastern slopes and parts of the low plateau, Fairchild covers the southeast corner of the plot and Swamp covers the central depression[44]. The soils drain freely except the Swamp soil and parts of the AVA soil, which encounter seasonal flooding in the wet season[26,44]. Soil water availability at 20 cm depth tends to be higher in gaps than in the understory, although shallower soils may be drier in gaps[41]. Wetter subsurface soils in gaps are likely caused by concentrated rainfall as drip lines from the edges of tree crowns, as well as higher rainfall in gaps and lower root density which decreases water extraction from the soil[41]. More detailed descriptions of the plot are given in Condit[39].

Soil moisture sampling. We collected soils during three periods in the 2015 dry season (February, March, and April) and one period in the 2016 dry season (March) (Fig. 2). The sampling periods were 6, 5, 10 and 8 days long, respectively. The 2016 dry season was associated with the 2015–2016 El Niño, and was the third longest dry season on BCI since 1954[29]. We took samples at a total of 363 sites, consisting of 200 seed trap sites along the trails of the 50-ha plot[45] and 163 other sites in the plot and around its border (Fig. 1). To reduce disturbance of the vegetation in the plot, we took most samples at the easily accessible seed traps: in all four sampling periods, we took one sample at 15 cm depth at each seed trap[45]. The seed traps cover all soil types[44] and major habitats in the plot except streamsides (cf. Harms *et al.*[43]). In April 2015 and in 2016 we took samples down to 40 cm depth at 100 sites along north-south transects in the plot, as well as at 41 sites with steep slopes (>15°) or rare habitats such as treefall gaps, the swamp and streamsides. Additionally, we took samples down to 100 cm depth at 22 sites around the plot perimeter in the three sampling periods in 2015. In total, we took 1299 samples that covered all soil types and habitats in the plot (Table 2). Finally, we assessed small-scale variation in soil moisture at eight seed traps by

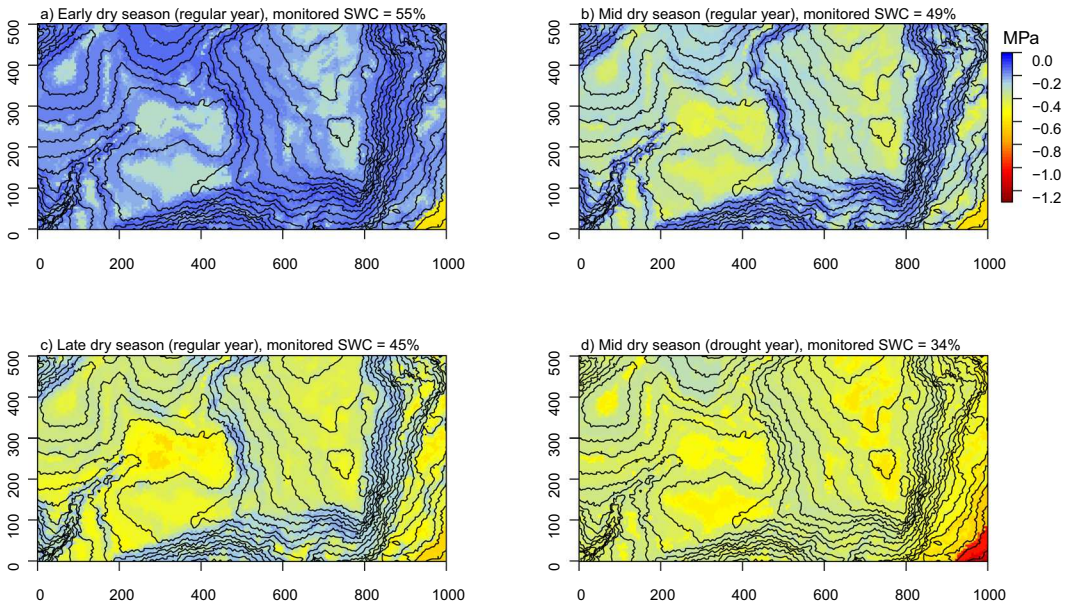

Fig. 3 Soil water potential (SWP) in the 50-ha plot on BCI. SWP is modelled with a Random Forest algorithm on a 5 m resolution at 15 cm depth and at 12 PM. SWP is shown for (**a**) early, (**b**) mid and (**c**) late dry season conditions for a regular year, and (**d**) mid dry season during a drought. Monitored soil water contents (SWC) correspond to the (**a**) 25th, (**b**) 50th and (**c**) 75th percentiles of monitored SWC during February, March and April from 1972 to 2018, and (**d**) median monitored SWC during our soil moisture measurements in March 2016, which was part of an El Niño drought. Basal area was fixed to the median basal area of the 5 × 5 m quadrats (0.03 m^2). Intervals of the contour lines are 2 m.

Filename	Type(s)	Description
BCI_Soil_moisture_mapping	.txt	Soil moisture data used for mapping
BCI_Soil_moisture_small_scale	.txt	Soil moisture data used for assessing small scale variation
BCI_ Soil_moisture_R_code	.R	R code for creating maps
BCI_soil_type	.txt	Soil type map digitized from Baillie *et al.*[44]
BCI_SWP_RF_model	.RData	Random Forest model (rfsrc object in R)
BCI_SWP_map_early_dry_season_regular BCI_SWP_map_mid_dry_season_regular BCI_SWP_map_late_dry_season_regular BCI_SWP_map_ mid_dry_season_drought	.txt,.pdf,.tif	Maps of soil water potential as presented in Fig. 3

Table 3. List of data records. All data are available from Figshare[52].

taking samples at 15 cm depth at the trap and two samples per distance class from the trap (1, 2 and 4 meters) in random compass directions.

We collected the soil samples with 1–3 cm diameter soil augers, depending on the sampling depth. We inserted the auger into the soil until the depths mentioned above. We sealed the lowest 1 cm of the soil core in airtight plastic vials for soil water potential measurements and the 9 cm above it in zip lock bags for soil water content measurements. Then we transported the samples to the laboratory in insulating containers with cooling elements. In the lab, we measured soil water potential (SWP) for each sample with a WP4C Dewpoint PotentiaMeter (Decagon Devices, Inc., Pullman WA, USA). We also assessed soil water content (SWC) gravimetrically for each sample from fresh mass (f) and dry mass (d) determined after 72 hours at 105 °C (SWC = (f − d)/d).

Predictors. We used seven predictors to model SWP throughout the 50-ha plot (Table 1). We derived elevation and slope on a 5 m resolution from a digital elevation model[46]. We also digitized a map of soil type on a 5 m resolution from a survey report on BCI soils[44]. On the coarse soil survey map, the seasonal swamp was shifted northwards compared to the more detailed habitat map of Harms *et al.*[43]. We assigned the Swamp soil type to the area defined as swamp in the habitat map and assigned the soil type surrounding the swamp (Marron) to the area north of the newly defined swamp. Additionally, we summed and ln-transformed basal area in each 5 × 5 m subquadrat for all trees ≥1 cm diameter at breast height in the 2015 tree census[36] to account for the effect of vegetation density and treefall gaps on water availability. We also accounted for variation in SWP caused by the ln(depth) and time of sampling.

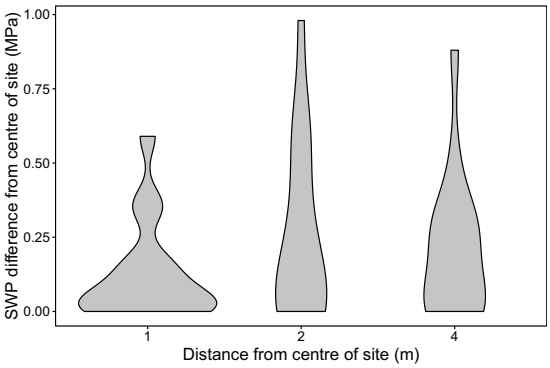

Fig. 4 Small scale variation in soil water potential (SWP). Graphs show the difference between SWP in the centre of a site ($n = 8$) and SWP measured at 1, 2 or 4 meters from the centre in a random compass direction. The 10th, 50th and 90th percentiles of the differences in SWP per distance are 0.00, 0.06 and 0.36 MPa for 1 m distance, 0.00, 0.14 and 0.61 MPa for 2 m distance and 0.00, 0.15 and 0.41 MPa for 4 m distance, respectively.

To assess temporal variation of SWP caused by differences in drought intensity, we used SWC monitoring data collected by the Smithsonian Tropical Research Institute every one to two weeks at 10 locations in a catchment 1.25 km from the 50-ha plot[47]. We calculated the mean SWC for each monitoring day, and calculated SWC for our sampling days by linear interpolation between SWC of the monitoring days. Although SWC from our soil samples was slightly lower than monitored SWC, probably due to different soil types and flatter terrain in the 50-ha plot, the temporal trend was similar (Fig. 2). Monitored SWC also accounted for rainfall during sampling. There were four days with light showers on BCI during the sampling periods, two of which had sufficient rain (5 mm on 8 April 2015 and 1 mm on 17 March 2016) to reach the forest floor (>0.5 mm)[48]. Monitored SWC increased in the week of 8 April 2015 and started to decline less steeply in the week of 17 March 2016 (Fig. 2). We compared SWP predictions using monitored SWC versus cumulative water deficit (a water balance based on rainfall and evapotranspiration) as an alternative indicator of drought intensity. We found that monitored SWC captured the severe drought in 2016 well whereas cumulative water deficits in 2016 were less negative than expected, probably due to the incomplete saturation of the soil during the previous wet season.

Random Forest modelling and mapping. We modelled SWP using Random Forests (RF)[30]. RF is a machine learning method that aggregates many decision trees (simple models that use binary splits to relate a response to predictors) that are constructed with a bootstrapped sample of the data for each tree and a random subset of the predictors[49]. RF performs well relative to similar algorithms and is robust to overfitting, noise and uneven spatial sampling[30,49,50]. We compared RF with Boosted Regression Trees, another algorithm known for its high predictive performance[51]. We found little difference in performance but smoother fits between SWP and the predictors in RF compared to BRT, indicating less overfitting in RF.

After assessing goodness of fit (see Technical Validation), we used the RF model to map SWP. For slope, elevation and soil type, we determined the nearest data point to the centre of each 5 × 5 m quadrat in the 50-ha plot. Basal area was set to the median across the plot (0.03 m^2 per 5 × 5 m quadrat). As soil moisture varies strongly during the dry season, we created maps of soil water potential for various levels of dry season intensity (see Data Records).

Data Records

All data are freely available from Figshare[52]. We provide soil moisture sampling data and soil water potential maps for early, mid and late dry season conditions during a regular year and for mid dry season conditions during a severe drought (Fig. 3). The maps are provided as pdf files, text files and TIFF images to facilitate viewing, analyses and visualization in various software packages (Table 3). We also provide the Random Forest model and the soil type map we digitized from Baillie *et al.*[44] for users creating custom maps (Table 3). All other data needed for creating custom maps are freely available through the links in the code. Finally, we provide data on small-scale soil moisture variation (Fig. 4).

Technical Validation

We estimated the goodness of fit of the Random Forest model using out-of-bag (OOB) data, which performs similarly to setting aside a test set[30]. For each bootstrapped iteration, the model used the tree that was created based on the bootstrapped sample to predict SWP for the data that was not in the bootstrapped sample (i.e. the OOB data, comprising around one-third of the observations per iteration)[49]. For each SWP observation, the mean predicted SWP across iterations was used to calculate error metrics[30]. The proportion of variance explained by the model (R^2) for all sampling periods combined was 0.41, the Root Mean Squared Error (RMSE) was 0.30 MPa and the Mean Absolute Error (MAE) was 0.23 MPa (Fig. 5a). Predictions were particularly accurate for April 2015 ($R^2 = 0.51$, Fig. 5g). Predictions were less accurate for February 2015 ($R^2 = 0.31$, Fig. 5c) and for March 2016 ($R^2 = 0.14$, Fig. 5h). After assessing goodness of fit, we predicted SWP with the full model, i.e. with the aggregated trees (Fig. 5, left panels). Variance explained was higher and errors were lower in the full model compared to the

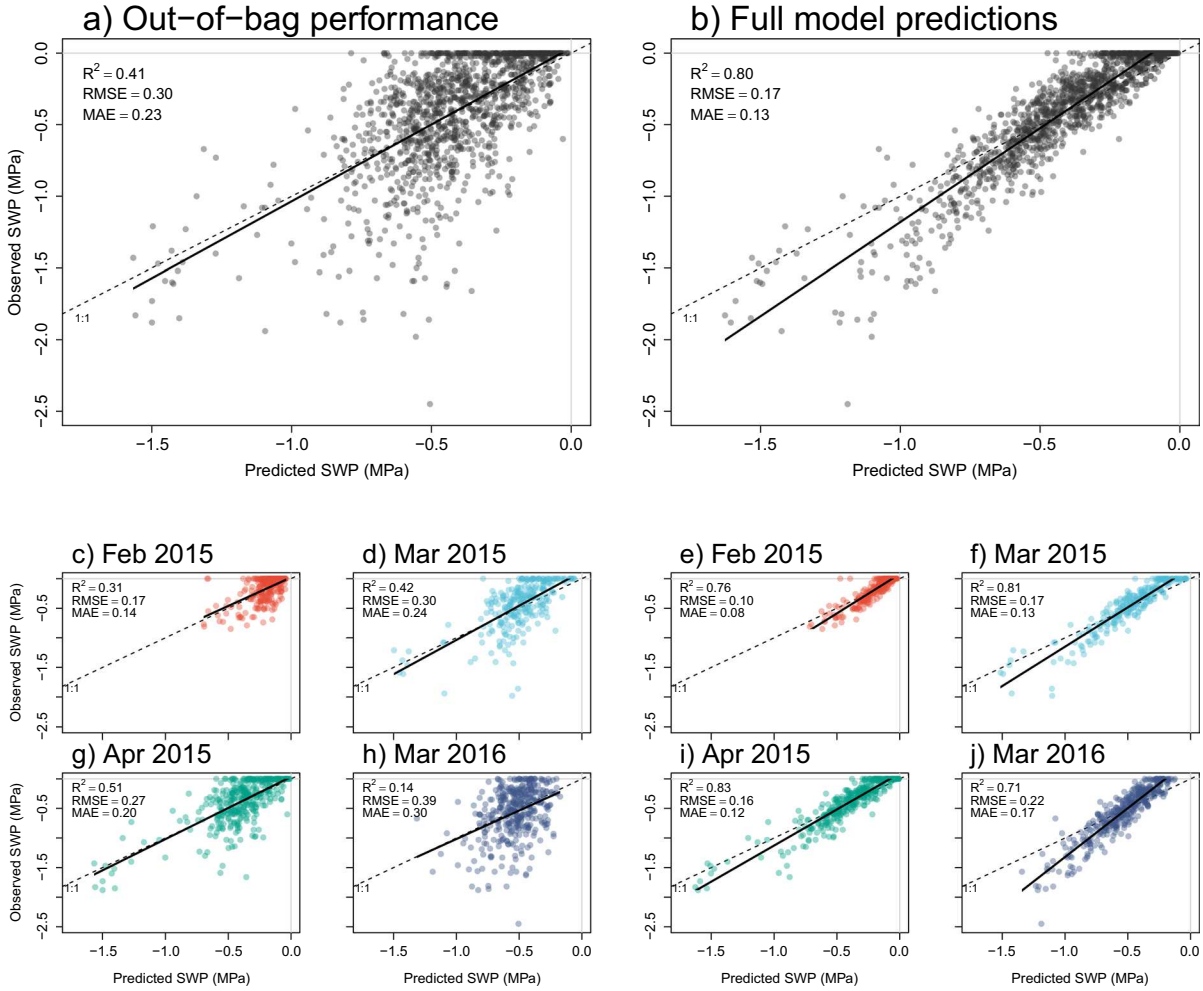

Fig. 5 Observed soil water potential (SWP) versus SWP predicted by the Random Forest (RF) model. (**a**) We assessed model performance from the single decision trees that were fitted on a bootstrapped sample to predict SWP for the out-of-bag data (see Technical Validation for details). (**b**) We made predictions of the full model based on the aggregated decision trees. We also show performance (**c**,**d**,**g**,**h**) and predictions (**e**,**f**,**i**,**j**) of the same RF model for the separate sampling periods.

OOB values (Fig. 5b). However, note that the OOB values should be used to estimate model performance[30,49]. The full model slightly overestimated SWP in the lower SWP range (predicted SWP was slightly higher than observed), particularly for the El Niño drought in March 2016 (Fig. 5j). The lowest SWP we measured was −2.45 MPa in March 2016 (see Fig. 5h), which was similar to the lowest value measured in the plot (−2.3 MPa) during the relatively dry 1985 dry season[41].

The importance of predictors and their relationship with SWP was generally as expected (Fig. 6). SWP was most strongly related to monitored soil water content; SWP in the 50-ha plot increased (i.e. soils were wetter) with increasing soil water content at the monitoring location (Fig. 6a). Soil type had a strong influence on SWP as well. Fairchild soil in the southeast corner of the plot was much drier than the other soil types (Fig. 6b). Fairchild soil that we sampled had a distinct white to yellow colour, it drains freely and is the only soil in the 50-ha plot that is not derived from andesite parent material[44]. AVA and Swamp soils were wetter than Marron soil, likely because they encounter seasonal flooding[44]. We expected the swamp to be even wetter than our model predicted (see flat area in the centre of the plot in Fig. 3). There are two likely reasons for the drier predictions in the swamp. First, we took most measurements in the swamp during the severe 2016 dry season (see Fig. 1), when the swamp largely dried out. Second, the swamp is mostly flat, and flat terrain was generally drier than slopes. Higher SWP on slopes (Fig. 6c) corresponded to earlier findings in the plot[41], indicating that the water table reaches the surface on the slopes around the edges of the relatively impermeable andesite cap under the high plateau[39,41,43]. High and low elevation sites were generally dry (Fig. 6d), likely because these elevations consist of two plateaus that are further from the water table than the slopes that connect them and because of the exceptionally dry Fairchild soil at low elevations.

Depth, time of sampling and basal area had a much weaker effect on SWP. SWP increased in deeper soil layers (Fig. 6d) and decreased in the course of the day as the soil dried out (Fig. 6e). SWP was higher in quadrats with high basal area (Fig. 6g), which contrasts with higher SWP in gaps versus understory measured at 20 cm depth at

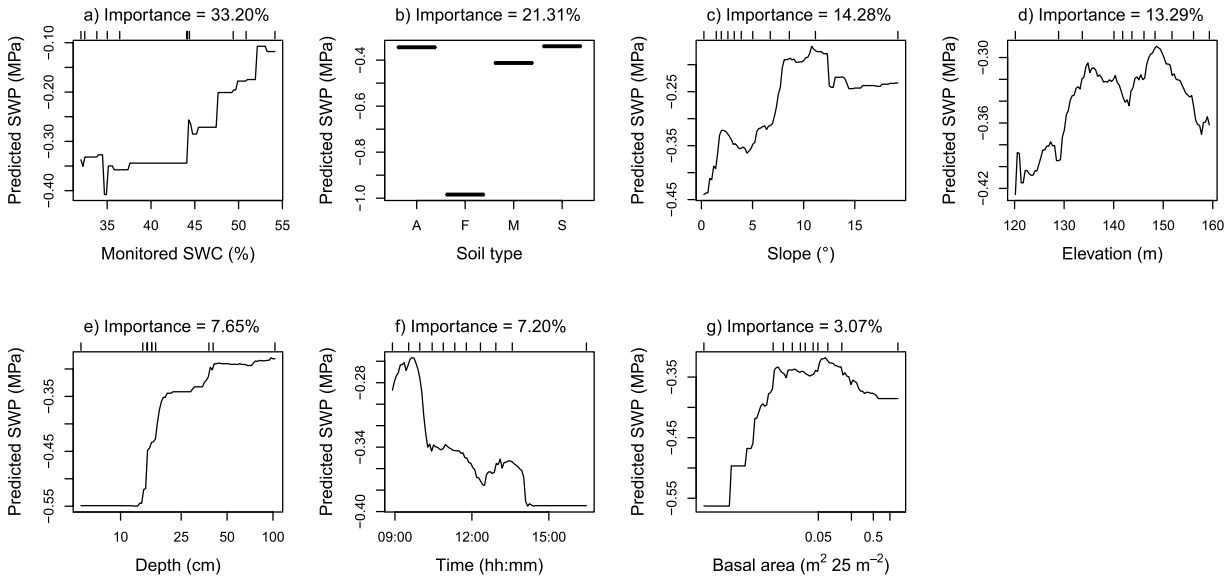

Fig. 6 Fitted values of soil water potential (SWP) versus predictors of the Random Forest model. Predictors are sorted based on their importance value. Ticks above the graphs indicate deciles of the predictor observations. Soil types are AVA (A), Fairchild (F), Marron (M) and Swamp (S)[44].

two locations in the 50-ha plot[41]. However, we measured SWP mostly at 15 cm depth and these surface soils may be drier in gaps[41]. Additionally, soil drying on BCI varies with gap size; evaporation is more important than water extraction from roots in large gaps whereas this is reversed in small gaps and in the understory[53], indicating that the relationship between canopy structure and soil moisture is complex.

Usage Notes

In addition to using the presented maps, users can adapt the provided code to produce maps for most dates (approximately from February until April) in any dry season starting from 1975, the year in which consistent monitoring of soil water content was started. The measurements in March 2016 covered the lowest levels of soil water content since monitoring started[47], so droughts can be mapped as well. The measurements did not cover wet seasons nor very early dry seasons (mid-December or January), so these periods cannot be mapped accurately. Soil water potential during these periods will be mostly saturated (0.00 MPa).

Code Availability

The code was written and annotated in R 3.4.1[54] and is available from Figshare[52]. The key package for implementing Random Forests was randomforestSRC 2.7.0[55].

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Acknowledgements

S.J.K. acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the Deutsch Forschungsgemeinschaft (DFG, German Research Foundation) – FZT 118. This project was conducted in the framework of the iDiv-Flexpool – the internal funding mechanism of iDiv. SK further acknowledges the support of A. Hildebrandt, yDiv (the graduate school of iDiv) and the Smithsonian Tropical Research Institute (STRI) through a Short-Term Fellowship. NR was funded by a research grant from the DFG (RU 1536/3-1). All authors acknowledge support from the DFG and Leipzig University within the program of Open Access Publishing. All authors further acknowledge constructive comments from two anonymous reviewers and thank the field assistants that collected the data.

Author Contributions

S.J.K. conducted the soil moisture measurements, constructed the maps and wrote the manuscript. All co-authors provided critical feedback and provided input on the writing.

Additional Information

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

3.2 Paper 2: Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

Kupers, S.J., Engelbrecht, B.M.J., Hernández, A., Wright S.J., Wirth C., Rüger, N. Journal of Ecology **107**:860–874 (2019). https://doi.org/10.1111/1365-2745.13096

Received: 14 March 2018 | Accepted: 18 October 2018

DOI: 10.1111/1365-2745.13096

RESEARCH ARTICLE

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: FZT 118 and RU 1536/3-1; Smithsonian Tropical Research Institute, Short-Term Fellowship

Handling Editor: Natalia Norden

Abstract

1. Local tree species distributions in tropical forests correlate strongly with soil water availability. However, it is unclear how species distributions are shaped by demographic responses to soil water availability. Specifically, it remains unknown how growth affects species distributions along water availability gradients relative to mortality.
2. We quantified spatial variation in dry season soil water potential (SWP) in the moist tropical forest on Barro Colorado Island, Panama, and used a hierarchical Bayesian approach to evaluate relationships between demographic responses of naturally regenerating seedlings to SWP (RGRs and first-year mortality) and species distributions along the SWP gradient for 62 species. We also tested whether species that were more abundant at the wet or dry end of the gradient performed better (a) at their "home end" of the gradient ("best at home" hypothesis) and (b) "at home" compared to co-occurring species ("home advantage" hypothesis).
3. Four and five species responded significantly to SWP in terms of growth or mortality respectively. Growth (but not mortality) responses were positively related to species distributions along the SWP gradient; species with a more positive (negative) growth response to SWP were more abundant at higher (lower) SWP, that is, at wetter (drier) sites. In addition, wet distributed species grew faster on the wet end of the SWP gradient than on the dry end ("best at home") and grew faster on the wet end than dry distributed species ("home advantage"). Mortality rates declined with seedling size for all species. Thus, seedling growth responses to SWP indirectly shaped local species distributions by influencing seedling size and thereby mortality risk.
4. *Synthesis.* By demonstrating how growth responses to spatial variation in soil water availability affect species distributions, we identified a demographic process underlying niche differentiation on hydrological gradients in tropical forests. Recognizing the role of these growth responses in shaping species distributions should improve the understanding of tropical forest composition and diversity along rainfall gradients and with climate change.

KEYWORDS
Barro Colorado Island, Panama, demographic responses, habitat associations, home advantage, niche differentiation, plant population and community dynamics, seedling performance, soil moisture

1 | INTRODUCTION

The distributions of tropical forest tree species respond strongly to regional rainfall gradients (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Condit, Engelbrecht, Pino, Pérez, & Turner, 2013; Esquivel-Muelbert et al., 2017). At the local scale, species distributions are often associated with topographic or edaphic habitats that vary in soil water availability (Chuyong et al., 2011; Gunatilleke et al., 2006; Harms, Condit, Hubbell, & Foster, 2001), and these habitat associations tend to become stronger through ontogeny (Comita, Condit, & Hubbell, 2007; Paoli, Curran, & Zak, 2006; Webb & Peart, 2000). This is likely due to differential mortality responses to soil water availability among species, starting at the seedling stage (Comita & Engelbrecht, 2009; Engelbrecht et al., 2007). Yet, the exact mechanism by which demographic responses to soil water availability lead to spatial partitioning of soil water gradients (i.e., hydrological niche differentiation) remains unclear (Silvertown, Araya, & Gowing, 2015).

There are at least two possibilities by which seedling demography may shape species distributions along soil water gradients. Water shortage might shape species distributions directly by increasing drought-induced seedling mortality (Comita & Engelbrecht, 2009, 2014). Alternatively, water shortage might shape distributions indirectly by decreasing seedling growth, leading to smaller sized seedlings that suffer higher mortality rates (Delissio & Primack, 2003; Gilbert, Harms, Hamill, & Hubbell, 2001; Johnson, Condit, Hubbell, & Comita, 2017; Rose & Poorter, 2003). Our goal is to determine if mortality or growth responses to soil water availability (or both) shape local species distributions.

Recently, Fortunel et al. (2016) proposed a framework to understand how differential species performance (growth or mortality) among habitats with contrasting abiotic or biotic conditions shapes associations to those habitats. The authors posed two hypotheses. First, species might perform better in their "home habitat" than in other habitats (henceforth "best at home" hypothesis). Second, species might perform better "at home" than species that are not associated with that habitat (henceforth "home advantage" hypothesis).

With respect to water availability, reciprocal transplant experiments have implicitly tested these two hypotheses by comparing seedling growth and mortality of species common to dry and wet forests along a rainfall gradient in central Panama. Dry forest species tended to perform best in dry forests (i.e., "best at home"), and wet forest species had lower mortality in wet forests but showed no clear pattern for growth (Brenes-Arguedas, Coley, & Kursar, 2009; Gaviria & Engelbrecht, 2015; Gaviria, Turner, & Engelbrecht, 2017). Wet forest species generally grew faster than dry forest species not only in wet forests (i.e., they had a "home advantage") but also in dry forests, indicating that wet forest species have inherently higher growth rates. In contrast, dry forest species had a "home advantage" in terms of lower mortality, suggesting that they invest more in adaptations to survive drought than wet forest species, which might trade-off against their ability to achieve high growth rates (Brenes-Arguedas, Roddy, & Kursar, 2013).

Despite our increasing understanding of performance differences between species from contrasting forest environments, the performance of naturally regenerating co-occurring seedlings with respect to soil water availability has only been compared once at a local scale (Comita & Engelbrecht, 2009). Moreover, studies linking local performance or species distributions to soil water status in tropical forests either used topographic or edaphic habitats as a proxy for soil water availability (see, e.g., Baltzer, Davies, Noor, Kassim, & LaFrankie, 2007; Chuyong et al., 2011; Comita & Engelbrecht, 2009; Daws, Pearson, Burslem, Mullins, & Dalling, 2005; Engelbrecht et al., 2007) or measured soil water content (Ashton, Gunatilleke, & Gunatilleke, 1995; Baraloto & Goldberg, 2004; De Gouvenain, Kobe, & Silander, 2007; Uriarte, Muscarella, & Zimmerman, 2018, but see Webb & Peart, 2000). However, soils with similar soil water contents can differ widely in their capacity to supply water to plants depending on their texture (Juo & Franzluebbers, 2003). Plants draw water from the soil along the soil–plant–atmosphere continuum of water potential (Lambers, Chapin, & Pons, 2008). Hence, soil water potential (SWP) is the most relevant measure of water status for plant–water relations and performance, especially during periods when water availability is limiting (Juo & Franzluebbers, 2003). Yet, few studies measured SWP at the spatial and temporal scales necessary to link SWP to performance or species distributions.

We explored how demographic responses to soil water availability shape species distributions. We constructed a detailed spatial gradient of SWP at 200 seedling census sites on Barro Colorado Island (BCI), Panama. We measured SWP during two dry seasons including a strong El Niño dry season, thereby capturing SWP during a drought event that could have severe effects on seedling dynamics (Comita & Engelbrecht, 2014). We used 21 years of annual seedling censuses to quantify local species distributions along the SWP gradient and to estimate species-specific growth and first-year mortality responses to SWP. Specifically, we ask:

1. Are species distributions along the SWP gradient related to growth and/or mortality responses to SWP? We expect that species differ strongly in their drought sensitivity (Brenes-Arguedas et al., 2009; Engelbrecht & Kursar, 2003), and that drought-sensitive species with positive demographic responses

to SWP are associated with wetter parts of the SWP gradient (Engelbrecht et al., 2007).

2. Do species perform "best at home", that is, better at the end of the SWP gradient to which they are associated? We expect that species associated with wetter sites perform "best at home" (i.e., have higher growth and lower mortality rates under wetter conditions), whereas species associated with drier sites are drought tolerant and indifferent to SWP (Comita & Engelbrecht, 2009).
3. Do species have a "home advantage," that is, better performance at their end of the SWP gradient than species associated with the other end? In terms of growth, we expect that wet distributed species have a "home advantage" over dry distributed species due to inherently higher growth rates (Brenes-Arguedas et al., 2009; Gaviria et al., 2017). In contrast, we expect that dry distributed species have a "home advantage" in terms of mortality, due to adaptations to cope with drought (Brenes-Arguedas et al., 2013).

By testing how growth and mortality responses to soil water availability are linked to species distributions, we explored the demographic underpinnings of niche differentiation on fine-scale soil moisture gradients in a tropical forest (Silvertown et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in a 50-ha Forest Dynamics Plot (Hubbell & Foster, 1983) located in old-growth, semideciduous lowland moist forest on Barro Colorado Island (BCI), Panama (9.15°N, 79.85°W). Annual rainfall averages 2,660 mm, 10% of which falls in the dry season from mid-December to late April (STRI, 2018). The intensity and length of the dry season vary greatly among years, with especially long dry seasons during some El Niño events (Condit et al., 2004). The 50-ha plot lies on a relatively flat plateau (elevation ranges from 120 to 155 m a.s.l, Hubbell & Foster, 1983). Soil water availability varies with topography within the 50-ha plot, with slopes being wetter than plateaus (i.e., SWPs are less negative, Becker, Rabenold, Idol, & Smith, 1988; Daws, Mullins, Burslem, Paton, & Dalling, 2002).

2.2 | Data collection

We focused on 200 permanent seedling census sites (henceforth sites) within the 50-ha plot (Wright, Muller-Landau, Calderón, & Hernandéz, 2005). The sites cover all topographic habitats within the 50-ha plot except streamsides (cf. Harms et al., 2001, see Supporting Information Figure S1.1 in Appendix S1). Each site has three 1-m^2 seedling plots (600 plots in total), located 2 m from the centre of the site. We tagged every seedling of woody species, identified them to species, measured their heights, and recorded mortality annually from 1994 to 2014 (see Wright et al., 2005, for methods).

To quantify spatial variation in soil water status, we took soil samples at 15 cm depth at each of the seedling census sites and measured SWP with a WP4C Dewpoint PotentiaMeter (Decagon Devices, Inc., Pullman WA, USA). We made these measurements in the dry season, when water availability becomes limiting for seedling growth and survival (Comita & Engelbrecht, 2009). We measured SWP three times in the 2015 dry season (February, March, and April) and once in the 2016 dry season (March). The 2016 dry season was the third longest dry season recorded on BCI since 1954 and was associated with the 2015–2016 El Niño (STRI, 2018). No rain occurred during sampling except in April 2015, and we excluded samples taken after the rain in that sampling round. After measuring SWP, we used the same soil samples to assess soil water content (SWC) gravimetrically from fresh mass (f) and dry mass (d) determined after 72 hr at 105°C (SWC = (f – d)/d). We excluded six outliers in SWP by comparing measured SWP and SWC with soil water retention curves we constructed for a subsample of the sites (see Supporting Information Appendix S2). We then calculated the median SWP for each site to characterize dry-season soil water status.

To determine whether spatial variation in SWP persisted over time, we evaluated correlations of site-specific SWP values across the four sampling rounds. To determine whether our measurements captured the peak of the dry season, which should be most limiting for seedling performance, we compared our SWC measurements with SWC measurements taken every 2 weeks at a second location on BCI, 1.25 km from the 50-ha plot (STRI, 2018). To determine whether our SWP measurements at 15 cm depth were representative of SWP in deeper soil layers, we took additional samples at 40 and 100 cm depth for 36 census sites and 66 sites adjacent to the 50-ha plot and correlated SWP at these depths with SWP at 15 cm.

2.3 | Species distributions along the SWP gradient

We quantified species distributions as distributional centres and spread along the SWP gradient for all 62 species included in the growth or mortality models (see Section 2.4). We defined centre and spread as the median and standard deviation (*SD*), respectively, of SWP at the sites where seedlings of a species occurred. We calculated centre and spread for each annual census individually and for all seedling observations across all censuses collectively. Values varied widely for individual censuses, especially for rare species that sometimes had only one individual in a census (Supporting Information Figure S1.2). For this reason, we believe values calculated over all censuses best represent species distributions, although we recognize that individuals that persisted across censuses have a stronger influence on this measure of species distributions than individuals that died quickly. We present distributions calculated over all censuses in the main text. Analyses using distributions calculated from single censuses (see Section 2.4) gave similar results (see Section 3.3).

To test whether species distributions along the SWP gradient differed significantly from random distributions, we compared the observed distributional centre and spread of each species with distributions generated by three increasingly conservative null models. In the first null model, we randomly assigned individuals of each species to sites 1,000 times, while keeping all observations of an individual together. In the second null model, we kept individuals

that occurred at the same site together and randomly assigned these individuals to sites 1,000 times, which retained site-level clumping of conspecifics. In the third null model, we preserved the spatial autocorrelation of species distributions by shifting all individuals from one site to the next along the trail network 200 times (because there are 200 sites). For each null distribution, we calculated distributional centres and spread of species as described above. If the observed distributional centre of a species was below the 2.5th or above the 97.5th percentile of the distributional centres of the null distributions, the species was associated with dry or wet sites respectively. Similarly, if the observed distributional spread was below the 2.5th or above the 97.5th percentile of the distributional spreads of the null distributions, the species distribution was more restricted or more widespread than expected by chance respectively.

We also determined whether species distributions with respect to soil water availability were consistent across life stages. To do this, we evaluated correlations between our distributional centres along the SWP gradient and associations with wet vs. dry habitats for larger seedlings and saplings (≥20 cm tall and <1 cm dbh) and trees (≥1 cm dbh). Comita et al. (2007) determined the density of larger seedlings and saplings and trees in each 20 × 20 m quadrat in the 50-ha plot, calculated average densities for the five topographic habitats of Harms et al. (2001), and standardized by the average density across all 50 ha for each species. Following Engelbrecht et al. (2007), we used these data to calculate relative densities pooled over three wet habitats (slopes [sl], streamsides [st], and the swamp [sw]) vs. two drier habitats (high plateau [hp] and low plateau [lp]). The calculation follows:

$$\ln\left(\sqrt{\frac{w_{sl}*d_{sl}+w_{st}*d_{st}+w_{sw}*d_{sw}}{w_{hp}*d_{hp}+w_{lp}*d_{lp}}}\right) \quad (1)$$

where d_{xx} is the standardized density in habitat xx and w_{xx} is the fraction of the pooled dry or wet habitat covered by habitat xx (e.g., w_{sl} equals the area in slope habitat divided by the sum of the areas in slope, streamside, and swamp habitats, data from Harms et al., 2001). Compared with the original calculation from Engelbrecht et al. (2007), we added the swamp to the wet habitats and log-transformed the habitat associations to reduce the influence of outliers with high relative densities in wet sites.

2.4 | Demographic responses to SWP and their link to species distributions

We quantified growth as annual relative height growth rate (RGR, henceforth growth):

$$\mathrm{RGR}=\frac{\ln(\mathrm{height}_2)-\ln(\mathrm{height}_1)}{t_2-t_1} \quad (2)$$

where height_2 and height_1 are the annual height measurements at times t_2 and t_1 respectively. We quantified mortality (dead/alive) in the census in the year after each seedling was first recorded (first-year mortality, henceforth mortality). We excluded seedlings that had resprouted, that were visibly damaged by animals, fallen branches, or leaf litter, or that were infected by pathogens, because this damage likely affected their performance more than variation in SWP. Additionally, we excluded observations made in a census interval that deviated more than a month from a full year (365 ± 30 days). In the growth model, we excluded (a) extreme positive outliers in growth likely caused by high-light levels (Wright et al., 2010) using a modified z-score (Iglewicz & Hoaglin, 1993), (b) individuals ≥2 m height as their height could not be accurately measured, and (c) growth ≤0 (see below for details). We included all shrub and tree species with ≥100 growth observations in the growth model, and all species with ≥100 first-year seedlings in the mortality model. We excluded two species that had >50% of their individuals at a single site. In total, we analysed demographic rates for 62 species; the growth model included 53 species with 16,834 individuals (50,901 growth observations) and the mortality model included 43 species with 31,246 individuals.

We assessed growth and mortality responses to SWP and their link to distributional centres with two-level Bayesian models. In the growth model, the first (individual-level) regression predicted growth across individuals for each species. Growth of individual i of species j at site s in year y ($\mathrm{pred}_{i,j,s,y}$) was predicted from height at the beginning of the census interval ($H_{i,y}$) and median SWP ($\mathrm{SWP}_{i,s}$) where the individual occurred:

$$\mathrm{pred}_{i,j,s,y}=\beta_{0,j}+\beta_{1,j}\times\mathrm{SWP}_{i,s}+\beta_{2,j}\times\ln(H_{i,y})+u_i+u_s+u_y \quad (3)$$

where $\beta_{0,j}$, $\beta_{1,j}$, and $\beta_{2,j}$ described the species-specific mean log growth rate and the growth response to SWP and height, respectively, for species j. The model included random effects for individual (u_i), site (u_s), and year (u_y). We used a log-normal distribution to describe the variation in observed growth ($\mathrm{obs}_{i,j,s,y}$) around predicted growth:

$$\mathrm{obs}_{i,j,s,y}\sim\mathrm{lognormal}(\mathrm{pred}_{i,j,s,y}\sigma_{p,j}) \quad (4)$$

Mortality responses to SWP were modelled using a logistic version of Equation 3 and a Bernoulli distribution in Equation 4. The mortality model did not include a random effect for individual, because we evaluated mortality just once for each individual. For each species, we assessed the fit of the model by plotting growth and mortality observations and model predictions against SWP and height. Species responses to SWP and height were significant when their 95% credible interval (CI) excluded zero. We tested for an interaction between the effect of SWP and height, but the added interaction term ($\beta_{3,j}\times\mathrm{SWP}_{i,s}\times\ln(H_{i,y})$) was not significant for any species in the growth or mortality model.

The second (species-level) regression of the models related growth or mortality responses to SWP ($\beta_{1,j}$) to distributional centres observed along the SWP gradient (D_j) across species:

$$D_j\sim\mathrm{normal}(\gamma_0+\gamma_1\times\beta_{1,j},\sigma_d) \quad (5)$$

The Bayesian framework correctly accounts for uncertainty in $\beta_{1,j}$ (Clark, 2005; Ellison, 2004). To test if demographic responses were significantly related to the distributional centres (question 1,

see Section 1), we computed the 95% CI of the slope (γ_1). If the 95% CI did not include zero, the relationship was significant.

We ran additional Bayesian models to test if the link between demographic responses of species and their distributional centres (i.e., the species-level regression) was robust. To assess if relationships between growth responses to SWP and distributional centres emerged among first-year seedlings or only later, we ran a model with only first-year growth observations. This model also allowed for a more direct comparison with the first-year mortality results. We also tested for a potential bias in the relationship between demographic responses and distributions that might occur through an interaction between drought sensitivity of species and their vulnerability to pathogens or herbivory (Jactel et al., 2012; Oliva, Stenlid, & Martínez-Vilalta, 2014). To do this, we retained seedlings visibly damaged by animals or infected by pathogens in the growth and mortality models.

To detect a potential bias in the growth–distributions relationship resulting from excluding growth ≤0, we ran all growth models including growth ≤0. Negative growth can be caused by herbivory or falling debris (Delissio & Primack, 2003), die back caused by pathogens or drought (Gerhardt, 1996), or measurement error. Thus, many instances of negative growth are likely not a response to moisture availability. Positive growth most likely comes from faster growing seedlings that have a higher chance to survive and contribute to species distributions (Rozendaal, Brienen, Soliz-Gamboa, & Zuidema, 2010). Overall, models including only positive growth and models including growth ≤0 gave similar results, but as expected, including negative growth rates increased unexplained variation and diluted main effects (see Supporting Information Appendix S3).

Finally, we evaluated whether calculating distributional centres based on single censuses vs. all observations across all censuses affected relationships between demographic responses and distributional centres. To do this, we performed 10 growth and mortality models with distributional centres calculated from the 10 single censuses with the most individuals and included species with ≥20 individuals in the selected census. We also performed growth and mortality models for the median of distributional centres of all single censuses.

For each growth and mortality model, we calculated the proportion of explained variance (R^2) following Gelman and Hill (2007) (Supporting Information Appendix S4.1). Additionally, we evaluated possible phylogenetic signal among the residuals of the species-level regression between distributional centres and demographic responses for each model. As there was no phylogenetic signal except for the first-year growth models, we did not consider it further (see Supporting Information Appendix S4.2 for details). Supporting Information Appendix S4.1 provides implementation procedures and model code. The Bayesian models were implemented in the Bayesian inference software package RSTAN version 2.16.2 (Stan Development Team, 2017).

2.5 | Testing the "best at home" and "home advantage" hypotheses

To evaluate the "best at home" and "home advantage" hypotheses (question 2 and 3, see Section 1), we first used our models to calculate growth and mortality for each species at a standardized size (10 cm height) at dry and wet sites. We defined dry and wet sites as the 10th percentile driest and wettest site along the SWP gradient, having median SWP of −0.75 MPa and −0.06 MPa respectively. We then classified species using three different thresholds. We classified species with a distributional centre among the 25%, 33%, or 50% of driest (or wettest) distributional centres as dry (or wet) distributed (see Figure 1). This classification does not imply that these species were significantly associated with the SWP gradient, which we tested separately using null models (see Section 2.3). To evaluate the "best at home" hypothesis, we compared performance "at home" (e.g., at dry sites for dry distributed species) and performance "away from home" (e.g., at wet sites for dry distributed species), using a paired *t*-test. For the "home advantage" hypothesis, we compared performance "at home" with performance "away from home" for the same sites (e.g., performance of dry distributed species and wet distributed species for dry sites respectively), using Welch's unequal variances *t*-test. We weighted both *t*-tests by the uncertainty in the calculated growth or mortality rates. For each species *j*, we determined these weights (weight_j) by drawing 1,000 random samples from the posterior distribution of $\beta_{0,j}$, $\beta_{1,j}$, and $\beta_{2,j}$ and calculating growth or mortality 1,000 times with these estimates as described above. We used the difference between the 2.5th and 97.5th percentile of these randomly fitted growth or mortality rates (width_j) as a measure of uncertainty and determined weights as:

$$\text{weight}_j = 1 - \frac{\text{width}_j}{\max(\text{width})} \quad (6)$$

The weight of the species with the largest uncertainty (i.e., largest width_j) was set to half the weight of the species with the second largest uncertainty (instead of zero). All analyses were conducted in R version 3.4.1 (R Core Team, 2017).

3 | RESULTS

3.1 | Soil water potential

SWP measurements ranged from −2.45 MPa to 0.00 MPa (saturation), and the medians per site ranged from −1.57 MPa to 0.00 MPa. Measurements taken at the same sites but during different sampling rounds were positively correlated among all rounds (February, March, April 2015, and March 2016, $p < 0.001$, Supporting Information Figure S1.3). Thus, relative differences in SWP were temporally consistent across sites and therefore likely reflected spatial variation throughout the seedling census period (1994–2014). Comparison of our SWC values with those from a nearby location where SWC is measured once every 2 weeks showed that we captured the peaks of the 2015 and 2016 dry seasons (Supporting Information Figure S1.4). SWP measurements were positively correlated across depths (15, 40, and 100 cm, $p < 0.001$, Supporting Information Figure S1.5), indicating that measurements at 15 cm depth represented variation in deeper soil layers.

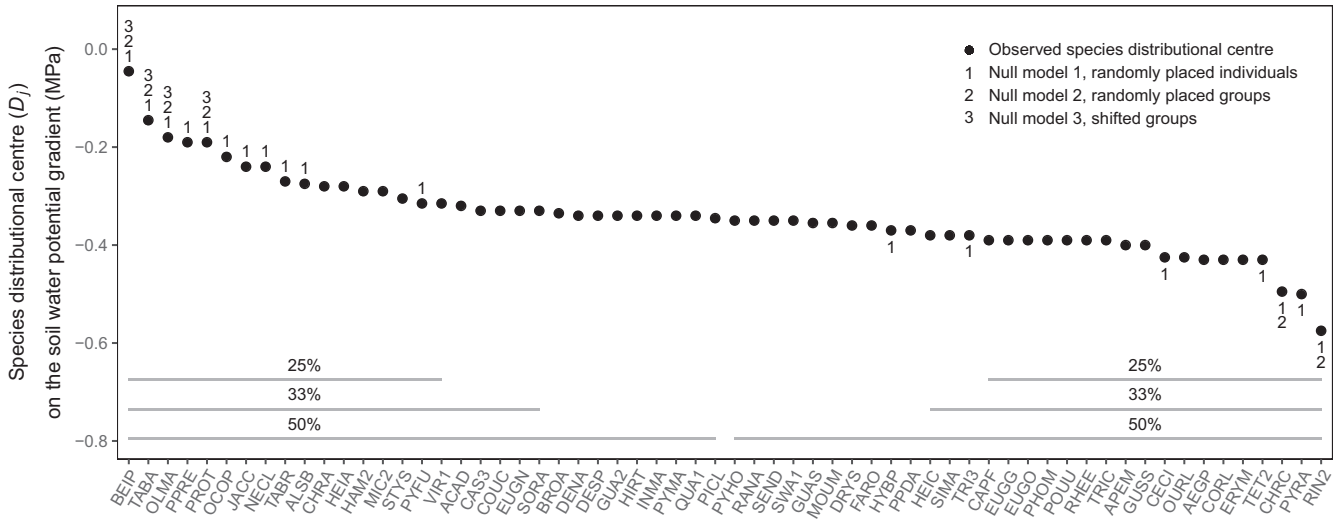

FIGURE 1 Distributional centres (D_j) of species on the local soil water potential (SWP) gradient. Species on the left side (SWP less negative) occur mostly on the wetter end of the gradient and species on the right side (SWP more negative) occur mostly on the drier end. Distributional centres are the median SWP of the sites where the seedlings of the respective species occurs. Numbers indicate species that have distributional centres outside of the 95% confidence interval of randomized values (see Section 2.3). Horizontal lines identify species with the wettest or driest 25%, 33%, or 50% of distributional centres. The 62 species each had ≥100 positive growth and/or ≥100 mortality records. Table S4 provides a key to full species names for the four-letter mnemonics along the horizontal axis

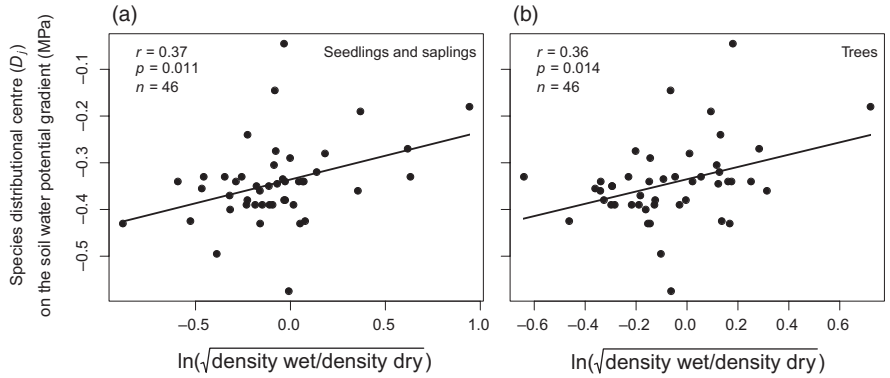

FIGURE 2 Relationships between relative densities of (a) seedlings and saplings (≥20 cm tall and <1 cm dbh) and (b) trees (≥1 cm dbh) in wet vs. dry habitats and seedling distributional centres on the soil water potential (SWP) gradient (i.e., median species distribution, D_j, see Section 2.3). Relative densities were calculated from densities in wet habitats (slopes, streamsides, and swamp combined) relative to dry habitats (high and low plateau combined, data adapted from Comita et al., 2007, see Equation 1 in Section 2.3). Solid lines represent significant relationships ($p < 0.05$).

3.2 | Distributional associations and demographic responses to SWP

Species' distributional centres along the SWP gradient ranged from −0.58 to −0.05 MPa (Figure 1, Supporting Information Table S4). Distributional centres of 18 of the 62 species (29.0%) differed significantly from random expectations using the first null model based on random shuffling of individuals, with 11 species being more abundant at wetter sites and seven species at drier sites (Figure 1). Likewise, 18 species exhibited significantly narrower or wider distributional spread along the SWP gradient (i.e., lower or higher *SD*) than expected, with 14 species being more restricted and four more widespread (Supporting Information Figure S1.6). Using the second and third null model, six and four species, respectively, had observed distributional centres that differed significantly from random distributions (Figure 1). Observed distributional spreads differed significantly from random expectations for four species in the second as well as in the third null model (Supporting Information Figure S1.6). Distributional centres of seedlings along the continuous SWP gradient were positively correlated with the relative densities of larger seedlings and saplings (≥ 20 cm tall and <1 cm dbh) and trees (≥ 1 cm dbh) in wet vs. dry habitats across the 50-ha plot (Figure 2, data from Comita et al., 2007).

Nine of the 62 species (14.5%) showed a significant demographic response to SWP (Supporting Information Figures S4

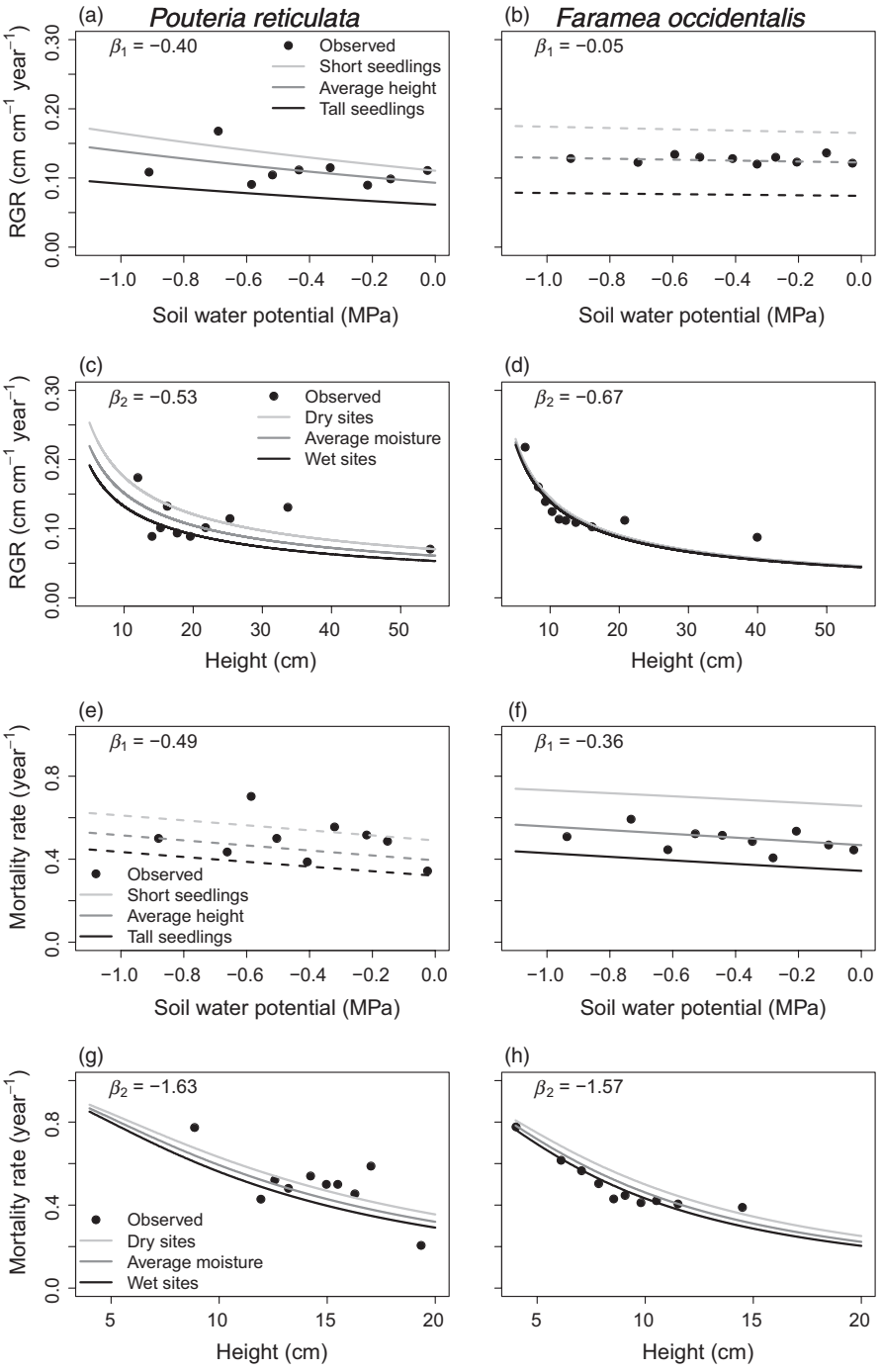

FIGURE 3 Relationships between RGRs (a–d), first-year mortality rates (e–h), and dry-season soil water potential (SWP; a, b, e, f) and seedling height (c, d, g, h) for seedlings of *Pouteria reticulata* (left panels) and *Faramea occidentalis* (right panels). Dots represent mean observed growth or mortality for 10 moisture (a, b, e, f) or 10 height (c, d, g, h) classes, each containing 10% of the individuals of the species. Lines show fitted growth and mortality responses to SWP for three levels of seedling height (short, average, tall; a, b, e, f), and responses to seedling height for three levels of SWP (dry, average, wet; c, d, g, h). Levels correspond to the 10th, 50th, and 90th percentile of height or SWP for each species. Solid lines indicate significant responses and dashed lines indicate non-significant responses. Each panel presents the fitted slope of the response (β_1 or β_2)

and S5). Four species responded significantly to SWP in terms of growth; three grew significantly slower with increasing moisture and one grew significantly faster (Supporting Information Table S5). Five species had significant mortality responses; four had lower mortality and one had higher mortality with increasing moisture (Supporting Information Table S6). None of the species responded significantly to SWP for both growth and mortality. In all species, growth and mortality decreased significantly with seedling height (Supporting Information Tables S5 and S6). Figure 3 illustrates demographic responses to dry season SWP and seedling height for two common species, one with significantly slower growth (*Pouteria reticulata*, Figure 3a) and one with significantly lower mortality (*Faramea occidentalis*, Figure 3f) at wetter sites. Over all species, the variation explained (R^2) was 0.30 for the growth model and 0.12 for the mortality model.

3.3 | The link between demographic responses and species distributions

The distributional centres of species along the SWP gradient were significantly positively related to growth responses to SWP (Figure 4a; γ_1 in Equation 5). Species with positive growth responses

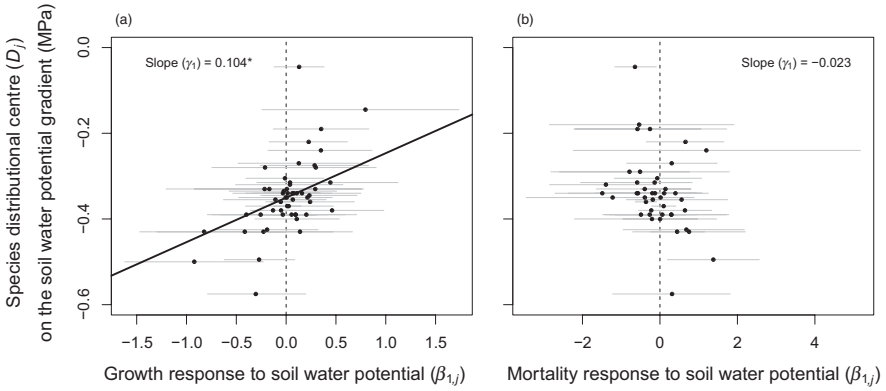

FIGURE 4 Relationships between distributional centres on the local soil water potential (SWP) gradient and (a) growth and (b) mortality responses of seedlings to SWP. Distributional centres on the SWP gradient are the median SWP of the sites where the species occurs (D_j, see Section 2). The growth and mortality responses are fitted species-specific slopes for relationships between SWP and each demographic rate ($\beta_{1,j}$, see text Equation 3). Horizontal grey lines represent the 95% credible intervals (CI) of $\beta_{1,j}$. The relationship between distributional centres and SWP responses is the slope of a linear regression fitted in the Bayesian models (γ_1, see text Equation 5), which is significant for growth rates (a) but not for mortality rates (b)

to SWP tended to have their distributional centres at wetter sites (higher SWP), and species with negative growth responses tended to have their distributional centres at drier sites (lower SWP).

In the models with only first-year growth, the positive relationship between distributional centres and growth responses was marginally significant (i.e., the 90% CI of γ_1 did not include zero, see Supporting Information Table S1.1). In the growth model that included observations with fungal infections or damage by animals, the relationship was significantly positive (Supporting Information Table S1.1). When including growth ≤0, the relationship was significant (and marginally significant) when seedlings affected by pathogens and herbivores were included (and excluded) and non-significant for only first-year growth (Supporting Information Figure S3.1, Supporting Information Table S1.1). Distributional centres were not related to first-year mortality responses to SWP (Figure 4b, Supporting Information Table S1.1).

Distributional centres based on single censuses were significantly or marginally significantly positively related to growth responses for seven of 10 censuses (Supporting Information Table S1.2). The relationship between mortality responses and distributional centres based on single censuses was only once marginally significantly negative, that is, species with a more negative mortality response to SWP expectedly tended to be more abundant at wetter sites (Supporting Information Table S1.2). The median of the distributional centres of all single censuses was significantly positively related to growth but not related to mortality (Supporting Information Table S1.2).

3.4 | The "best at home" and "home advantage" hypotheses

Wet distributed species grew significantly faster at wet sites than at dry sites (for all distribution thresholds; Figure 5a, Table 1). This is consistent with the "best at home" hypothesis. Dry distributed species did not grow faster at dry sites (Figure 5a, Table 1). The wettest distributed 33% and 50% of species grew significantly faster at wet sites than the driest distributed 33% and 50% of species, and the wettest distributed 25% of species grew marginally faster at wet sites than the driest distributed 25% of species (Figure 5b, Table 2). This is consistent with the "home advantage" hypothesis. Dry distributed species did not have a "home advantage" in terms of growth (Figure 5b, Table 2). Patterns weakened when negative growth was included (see Supporting Information Tables S3.1–S3.2 for details). For mortality, only the wettest distributed 50% of species performed marginally significantly better "at home" (Figure 5c, Table 1). We found no evidence for a "home advantage" for mortality (Figure 5d, Table 2).

4 | DISCUSSION

We explored the roles of growth and mortality responses to SWP in shaping local species distributions of naturally regenerating seedlings. Growth responses to SWP were positively related to distributional centres of species along the SWP gradient. Species that were more abundant at wetter sites grew faster there ("best at home") and outgrew species that were more abundant at drier sites ("home advantage"). In contrast, we found little evidence that first-year mortality responses to SWP affected species distributions. Instead, we propose that growth responses to SWP indirectly shape local species distributions, because growth advantages increase seedling size and thereby decrease mortality risk in later seedling stages. In this way, growth responses to SWP promote niche differentiation along gradients of soil water availability.

4.1 | Growth responses to soil water potential contribute to species distributions

As expected, we found that species with a more positive (negative) growth response to SWP were more abundant at wetter (drier) sites

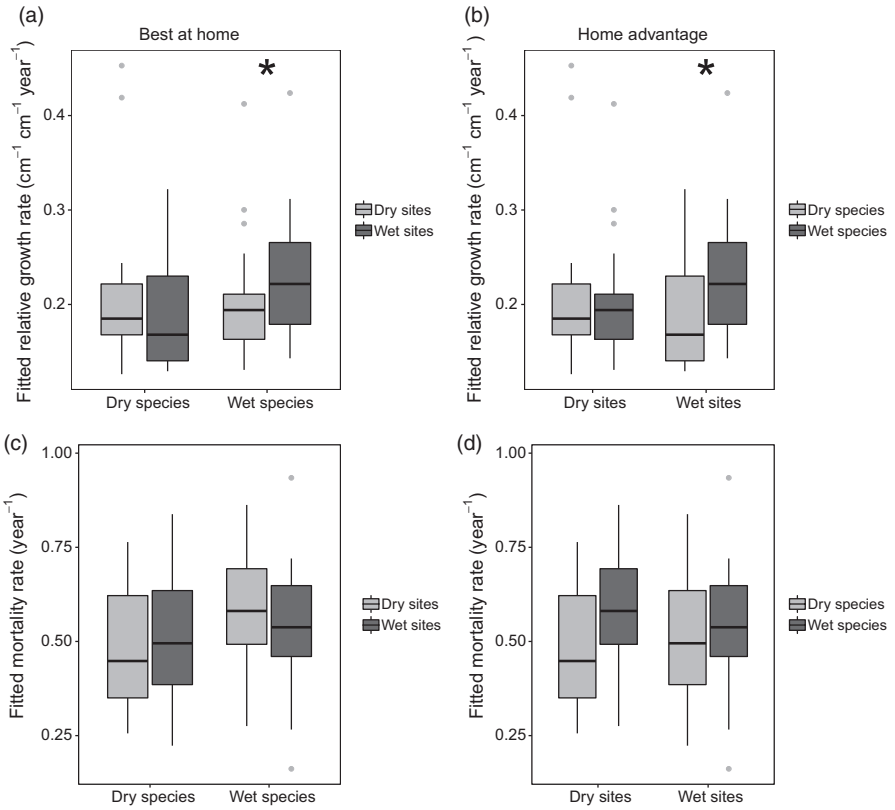

FIGURE 5 Tests of the "best at home" and "home advantage" hypotheses. For the "best at home" hypothesis (a, c), the box and whisker plots are for dry and wet distributed species (separated along the horizontal axis) and compare performance at dry vs. wet sites (light vs. dark shaded boxes, respectively). For the "home advantage" hypothesis (b, d), the box and whisker plots are for performance at dry or wet sites (separated along the horizontal axis) and compare performance of dry vs. wet distributed species (light vs. dark shading respectively). Shown is performance of dry and wet distributed species, which have a distributional centre that is among the 33% of driest or wettest distributional centres respectively (see Figure 1). Dry and wet sites were defined as the 10th percentile driest and wettest site along the soil water potential gradient respectively. Asterisks identify significant performance differences ($p < 0.05$). Tables 1 and 2 present results for the 25%, 33%, and 50% of driest and wettest distributed species.

(Figure 4a). In addition, species that were more abundant at wet sites grew faster "at home" (Figure 5a) and had a "home advantage" over dry distributed species (Figure 5b). Seedlings of species with such a growth advantage become taller than seedlings of species with slower growth. As we found that mortality rates declined rapidly with seedling height for all species (Green, Harms, & Connell, 2014; Rose & Poorter, 2003), a growth advantage allows seedlings to escape the vulnerable small seedling stage more rapidly (Kitajima & Fenner, 2000) than seedlings of other species. Experiments have documented species-specific responses of seedling growth to water availability (Ashton et al., 1995; Baltzer & Davies, 2012; Born et al., 2015; Bunker & Carson, 2005; O'Brien, Ong, & Reynolds, 2017; O'Brien, Philipson, Tay, & Hector, 2013; Yavitt & Wright, 2008). Our study is the first to show that differential growth responses of naturally regenerating seedlings contribute to local species distributions along a gradient of soil water availability.

The significant relationship between the growth responses of species to SWP and their distributional centres along the SWP gradient emerged from mostly non-significant growth responses to soil moisture at the within-species level. Just four of 53 species showed significant growth responses to SWP. There are several possible reasons for the lack of significant within-species responses. First, spatial differences in SWP among sites are likely subtle compared with other tropical forests due to the rather homogeneous topography of the BCI 50-ha plot (Brown et al., 2013; John et al., 2007). Second, seed dispersal limits seedling occurrence across the SWP gradient (Hubbell et al., 1999; Muller-Landau, Wright, Calderón, Condit, & Hubbell, 2008). For example, few seeds disperse to dry sites for species whose reproductive adults are restricted to wet sites. Dispersal limitation limits our ability to assess performance "away from home." Third, many species had relatively small overall sample sizes, which further increased uncertainty in SWP responses (Supporting Information Figure S1.7) and decreased the likelihood of detecting statistically significant responses (Supporting Information Figure S1.8). Nonetheless, the fitted slopes of the relationship between growth and SWP represent the best estimates of the magnitude of species' growth response to SWP (i.e., effect sizes, Nakagawa & Cuthill, 2007). These responses were significantly related to species distributions along the SWP gradient.

Surprisingly, three of the four species with significant growth responses to SWP grew slower at wetter sites. At wetter sites, higher pathogen pressure, anoxic conditions due to waterlogging in the wet

TABLE 1 Test of the "best at home" hypothesis. Shown are fitted growth or mortality rates of dry and wet distributed species at dry vs. wet sites. Bold values indicate significantly different mean performance ($p < 0.05$), and the italic value indicates marginally significantly different mean performance ($0.05 \leq p < 0.10$).

	Classification dry/wet species[a]	Dry sites[b]	Wet sites[b]			
		Mean (*SD*)	Mean (*SD*)	*t*	*df*	*p*
Growth						
Dry distributed species	50%	0.209 (0.077)	0.195 (0.059)	0.933	27	0.359
	33%	0.209 (0.087)	0.185 (0.056)	1.327	18	0.201
	25%	0.215 (0.093)	0.181 (0.048)	1.603	15	0.130
Wet distributed species	50%	0.209 (0.062)	0.228 (0.059)	−3.427	24	**0.002**
	33%	0.208 (0.071)	0.231 (0.068)	−2.915	16	**0.010**
	25%	0.203 (0.077)	0.237 (0.077)	−3.187	11	**0.009**
Mortality						
Dry distributed species	50%	0.478 (0.159)	0.494 (0.158)	−0.880	20	0.389
	33%	0.478 (0.172)	0.519 (0.172)	−1.724	13	0.108
	25%	0.492 (0.183)	0.534 (0.182)	−1.661	11	0.125
Wet distributed species	50%	0.544 (0.165)	0.498 (0.182)	1.800	21	*0.086*
	33%	0.577 (0.167)	0.536 (0.190)	1.396	14	0.184
	25%	0.611 (0.166)	0.578 (0.175)	0.897	11	0.389

[a]Each analysis was repeated contrasting the 25%, 33%, or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Figure 1). [b]Dry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient respectively.

TABLE 2 Test of the "home advantage" hypothesis. Shown are fitted growth or mortality rates of dry vs. wet distributed species at dry and wet sites. Bold values indicate significantly different mean performance ($p < 0.05$), and the italic value indicates marginally significantly different mean performance ($0.05 \leq p < 0.10$).

	Classification dry/wet species[a]	Dry distributed species	Wet distributed species			
		Mean (*SD*)	Mean (*SD*)	*t*	*df*	*p*
Growth						
Dry sites[b]	50%	0.209 (0.077)	0.209 (0.062)	−0.715	48.332	0.478
	33%	0.209 (0.087)	0.208 (0.071)	−0.676	29.170	0.504
	25%	0.215 (0.093)	0.203 (0.077)	−0.405	18.421	0.690
Wet sites[b]	50%	0.195 (0.059)	0.228 (0.059)	−2.106	49.759	**0.040**
	33%	0.185 (0.056)	0.231 (0.068)	−2.086	28.687	**0.046**
	25%	0.181 (0.048)	0.237 (0.077)	−1.805	16.468	*0.089*
Mortality						
Dry sites	50%	0.478 (0.159)	0.544 (0.165)	−1.358	40.665	0.182
	33%	0.478 (0.172)	0.577 (0.167)	−1.639	26.971	0.113
	25%	0.492 (0.183)	0.611 (0.166)	−1.607	21.999	0.122
Wet sites	50%	0.494 (0.158)	0.498 (0.182)	−0.202	39.462	0.841
	33%	0.519 (0.172)	0.536 (0.190)	−0.361	26.532	0.721
	25%	0.534 (0.182)	0.578 (0.175)	−0.836	21.924	0.412

[a]Each analysis was repeated contrasting the 25%, 33%, or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Figure 1). [b]Dry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient respectively.

season, or lower light conditions may limit growth (Brenes-Arguedas, Roddy, Coley, & Kursar, 2011; Gaviria et al., 2017; Lopez & Kursar, 2003; Spear, Coley, & Kursar, 2015). Indeed, sites with higher SWP were more shaded ($r = 0.27$, $p < 0.001$; Supporting Information Table S1.3, shade data from Condit, 2018). Thus, low light availability likely limited growth in wetter sites. Wetter sites also had lower

Mg ($r = -0.16$, $p = 0.03$) and N ($r = -0.25$, $p < 0.001$; Supporting Information Table S1.3, nutrient data from Wolf, Hubbell, Fricker, & Turner, 2015). However, a fertilization experiment near BCI showed that Mg did not limit seedling growth and that N only limited growth in combination with P (Santiago et al., 2012), suggesting that it is unlikely that lower Mg and N availability caused negative growth responses to higher SWP in the 50-ha plot.

Comita and Engelbrecht (2009) compared performance and distributions of larger seedlings (20–50 cm tall) for slopes (wet) and plateaus (dry) in the BCI 50-ha plot and found no evidence for the "best at home" and "home advantage" hypotheses for growth. We improved on their dichotomy of wet vs. dry sites. We used the most appropriate measure of soil water availability for plants (SWP) and resolved variation in soil water availability within plateaus and slopes (see Supporting Information Figure S1.1). This highlights the importance of small-scale soil moisture gradients in structuring plant communities (Araya et al., 2011).

Growth responses to water availability may also affect regional distributions of species along a rainfall gradient from the drier Pacific to wetter Caribbean coasts of central Panama. Although species common to dry forests in Southeast Asia and Amazonia often occur in wet forests as well (Baltzer et al., 2007; Esquivel-Muelbert et al., 2017), species turnover in Panama is strong, that is, dry forest species are often absent from wet forests (Condit et al., 2013; Jones et al., 2013; Pyke, Condit, Aguilar, & Lao, 2001). Reciprocal transplant experiments suggest that inherently slower growth rates may prevent dry forest species from colonizing wet forests in Panama (Brenes-Arguedas et al., 2009; Gaviria & Engelbrecht, 2015; Gaviria et al., 2017). Thus, wet forest species may have a "home advantage" in terms of growth over dry forest species at the regional scale.

4.2 | The role of mortality in shaping species distributions

Unexpectedly, the distributions of species along the SWP gradient were not related to first-year mortality responses to SWP (Figure 4b). We also found little evidence for species having lower mortality rates "at home" (Table 1) and we found no evidence for a "home advantage" (Table 2). These results indicate that the role of first-year mortality responses to SWP in shaping species distributions was relatively minor, even though experiments suggest that first-year mortality influences distributions with respect to variation in water, nutrient, and light availability (Baltzer & Davies, 2012; Engelbrecht & Kursar, 2003; Engelbrecht, Kursar, & Tyree, 2005; Lucas, Bruna, & Nascimento, 2013). Contrasting with our results, larger seedlings (20–50 cm tall) of dry-associated species had lower mortality than wet-associated species in the same 50-ha plot, particularly on the dry plateau (i.e., "home advantage") in a severe dry season (Comita & Engelbrecht, 2009).

There are several possible explanations for why we did not find a clear link between mortality responses to SWP and species distributions. First, our study spanned 21 years including many years with mild dry seasons, during which differences in mortality rates between dry and wet distributed species are likely less pronounced (Comita & Engelbrecht, 2014) than in years with severe dry seasons (Comita & Engelbrecht, 2009; Condit, Hubbell, & Foster, 1995). Accordingly, the population of drought-sensitive species may have recovered after droughts (Condit, Pérez, Lao, Aguilar, & Hubbell, 2017) at drier sites. Second, small seedlings are more vulnerable than tall seedlings to various causes of mortality besides resource availability, such as falling debris or herbivory (Rose & Poorter, 2003) and negative distance or frequency dependence (Green et al., 2014; Murphy, Wiegand, & Comita, 2017), which may have diluted the effect of water availability on mortality of the first-year seedlings in our study. Third, the annual censuses did not allow us to distinguish between dry and wet season mortality, which probably also diluted the signal of drought-induced mortality that is concentrated in the dry season (Comita & Engelbrecht, 2014).

4.3 | Implications for niche differentiation

We found evidence for spatial niche differentiation along the SWP gradient within the BCI 50-ha plot, as indicated by significant associations of distributional centres with the dry and wet end of the SWP gradient (Figure 1) and by the larger number of species with restricted rather than widespread distributions along the SWP gradient (Supporting Information Figure S1.6). However, in null models that took spatial clustering within and among sites into account, the number of significant distributional associations declined considerably. This indicates that dispersal limitation, often responsible for aggregation of individuals (Detto & Muller-Landau, 2013), caused seedlings of many species to occur in clumps that were not associated with the moisture gradient. Dispersal limitation, therefore, also played an important role in shaping the seedling distributions (Hubbell et al., 1999; Muller-Landau et al., 2008).

Seedling distributions along the SWP gradient were correlated with the distributions of larger seedlings and saplings and trees across wet slope vs. dry plateau habitats in the 50-ha plot (Figure 2), indicating that species associations to soil water availability arise early and hold across life stages. In contrast, previous studies found that habitat associations vary strongly between early and late life stages (Comita et al., 2007; Webb & Peart, 2000). However, these studies focused on significant topographic habitat associations of species (across life stages), whereas we compared relative positions on a soil water gradient (SWP and wet vs. dry habitats) among species. This allowed us to identify a consistent distributional signature of hydrological niche differentiation across life stages.

We speculate that a "home advantage" is a more important demographic signature of niche differentiation than "best at home" performance, because niche differentiation takes place when a species is superior to competitors at a specific location on a niche axis (Kawecki & Ebert, 2004; Silvertown, 2004). As we found a "home advantage" for growth but not mortality, this further suggests that growth responses to water availability shape species distributions along the SWP gradient.

5 | CONCLUSIONS

By quantifying a detailed gradient of SWP, we found that subtle interspecific differences in growth responses to SWP influenced species distributions across a naturally regenerating seedling community. Our findings emphasize the value of measuring small-scale spatial differences in SWP for studying the mechanisms driving hydrological niche differentiation. Future studies may test which traits that determine drought sensitivity, such as leaf water potential at turgor loss and embolism resistance (Anderegg et al., 2016; Bartlett, Scoffoni, & Sack, 2012), drive demographic responses to SWP. Such studies will improve predictions of compositional changes in tropical forests due to shifting rainfall patterns caused by climate change (Choat et al., 2018; IPCC, 2014).

ACKNOWLEDGEMENTS

SJK acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—FZT 118. This project has been conducted in the framework of the iDiv-Flexpool—the internal funding mechanism of iDiv. SK also acknowledges the support of A. Hildebrandt, yDiv (the graduate school of iDiv), the iDiv Open Science Publication Fund, and the Smithsonian Tropical Research Institute (STRI) through a Short-Term Fellowship. NR was funded by a research grant from the DFG (RU 1536/3-1). All authors acknowledge constructive comments from N. Norden and three anonymous reviewers, and thank the STRI staff that facilitated the project and the field assistants that collected the data.

AUTHORS' CONTRIBUTIONS

S.J.K., N.R., B.M.J.E., S.J.W., and C.W. conceived the study. S.J.W. and A.H. designed and performed the seedling censuses. S.J.K. conducted the soil water potential measurements, analysed the data, and wrote the manuscript with input from N.R., B.M.J.E., S.J.W., and C.W.

DATA ACCESSIBILITY

Soil moisture data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1023m1d (Kupers et al., 2018). Seedling data are available via ForestGEO (https://forestgeo.si.edu/research-programs/flowers-seeds-and-seedlings-initiative, ForestGEO, 2018). Hydrological and meteorological monitoring data are available from http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado (STRI, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Kupers SJ, Engelbrecht BMJ, Hernández A, Wright SJ, Wirth C, Rüger N. Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings. *J Ecol*. 2019;107:860–874. https://doi.org/10.1111/1365-2745.13096

3.3 Paper 3: Performance of tropical forest seedlings facing shade and drought: an interspecific trade-off in demographic responses

Kupers, S.J., Wirth, C., Engelbrecht, B.M.J., Hernández, A., Condit, R., Wright, S.J., Rüger, N. [In review at Scientific Reports]

Title page

Date: May 22, 2019

Journal: Scientific Reports

Title: Performance of tropical forest seedlings facing shade and drought: an interspecific trade-off in demographic responses

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Abstract

Seedlings in moist tropical forests must cope with deep shade and seasonal drought. However, the interspecific relationship between seedling performance in shade and drought remains unsettled. We quantified spatiotemporal variation in shade and drought in the seasonal moist tropical forest on Barro Colorado Island (BCI), Panama, and estimated responses of naturally regenerating seedlings as the slope of the relationship between performance and shade or drought intensity. Our performance metrics were relative height growth and first-year survival. We investigated the relationship between shade and drought responses for up to 63 species. There was an interspecific trade-off in species responses to shade versus species responses to dry season intensity; species that performed worse in the shade did not suffer during severe dry seasons and vice versa. This trade-off emerged in part from the absence of species that performed particularly well or poorly in both drought and shade. If drought stress in tropical forests increases with climate change and as solar radiation is higher during droughts, the trade-off may reinforce a shift towards species that resist drought but perform poorly in the shade by releasing them from deep shade.

Keywords

Barro Colorado Island, Panama; community dynamics; cumulative water deficit; drought tolerance; growth; seedling performance; survival; shade tolerance; soil water potential; trade-offs; tropical forest

Introduction

Differential performance of plant species along resource gradients affects species composition and contributes to species diversity[1-3]. Light and water are key resources for plants and a lack of light and water (i.e. shade and drought) strongly limits plant performance[4-6]. Yet, it remains unclear how shade and drought interact to shape performance of natural plant communities[7,8].

Smith and Huston[9] were the first to propose an interspecific trade-off between shade and drought tolerance, i.e. a shade tolerant species should be intolerant to drought and vice versa. They proposed various trade-offs in plant adaptations to cope with shade and drought, such as a trade-off in allocation to aboveground structures to increase light capture versus allocation to belowground structures to increase water uptake. Shade and drought tolerance traded off in a landmark study that determined shade and drought tolerance scores of species across the northern hemisphere[10]. However, other studies suggest that shade and drought tolerance may be unrelated[11,12] because traits that determine these tolerances do not require high resource allocation. For example, tolerance to shade is not directly related to high aboveground allocation but is instead promoted by slow growth and low specific leaf area[13]. Other traits reduce demand for light and water simultaneously (e.g. low respiration rates or low leaf nitrogen concentration), allowing for high shade and drought tolerance[14,15]. These traits contrast with traits promoting fast resource acquisition (e.g. low tissue density or high photosynthetic capacity), leading to the well-established fast-slow plant economic spectrum that predicts that traits related to shade and drought tolerance are positively related[16].

Various studies have evaluated the relationship between shade and drought tolerance in different ecosystems, but there is no conclusive answer as to which relationship emerges under which environmental conditions (see Table 1). Most of these studies used functional traits or

78 species distributions as proxies for shade and drought tolerance (Table 1), even though whole-
79 plant performance finally determines population dynamics[17]. The focus on traits is partly due to
80 the lack of small-scale data on light and water availability, which hinders evaluation of
81 performance differences within plant communities. This is particularly true for soil water
82 potential, which is the relevant measure of water status for plant performance[18] because plants
83 draw water from the soil along the soil-plant-atmosphere continuum of water potential[19]. As a
84 result, attempts to evaluate relationships between performance in shade and drought have been
85 limited to experiments (e.g. [11,14]). These experiments can only include a few species, making it
86 difficult to generalize performance trade-offs to species-rich natural communities.

87 The combined pressure of shade and drought is particularly evident in tropical forests[8].
88 As in other ecosystems, the relationship between light and water availability gradients in these
89 forests determines the adaptive pressures acting on plant communities. This relationship varies
90 depending on the scale at which the gradients are compared and local climatic conditions. In wet
91 and seasonal moist tropical forests, open vegetation or large gaps have lower soil moisture than
92 denser patches due to higher evaporation rates[20,21]. Similarly, less densely vegetated hilltops tend
93 to be drier than shaded valleys[22,23]. Thus, in these forests species would either need to cope with
94 low light or low soil moisture availability. Since these environmental differences are relatively
95 modest, one would expect a relatively weak interspecific trade-off between performance in
96 shaded versus dry conditions. When comparing relatively closed moist forests with relatively
97 open dry forests on a regional scale, there is a stronger contrast in environmental conditions
98 which should result in a stronger trade-off, i.e. in moist forests species are well adapted to shade
99 but poorly to drought, while in dry forests species are well adapted to drought but poorly to
100 shade[24]. Within tropical dry forests there is a pronounced division between evergreen species that

101 specialize on the dark understory and deciduous species that specialize on the bright canopy or
102 gaps[25]. Here there is a positive relationship between adaptation to shade and drought, i.e. a
103 division between conservative evergreen species that specialize on coping with shade and
104 drought and acquisitive deciduous species that avoid shade and take advantage of optimal
105 growing conditions in the wet season[25,26].

106 Temporal variation in shade and drought intensity also affects plant performance in
107 tropical forests. Light variation caused by gap dynamics are crucial for the establishment and
108 growth of many species[27]. Pronounced dry seasons and occasional, severe droughts strongly limit
109 growth and increase mortality[28,29]. Light availability in tropical forests is higher during droughts
110 due to increased solar radiation[30,31], which may also interactively affect performance.

111 Our objective was to study the relationship between demographic responses (growth and
112 survival) of naturally regenerating seedlings to spatiotemporal variation in shade and drought in
113 a moist tropical forest. Seedlings are particularly vulnerable to shade and drought because their
114 low biomass limits resource capture above and belowground[28,32]. We evaluated species responses
115 to shade and drought as the slope between seedling performance (growth or survival) and shade
116 or drought intensity for a large community of woody seedlings on Barro Colorado Island (BCI),
117 Panama. To this end, we determined shade intensity at 200 seedling census sites across years (i.e.
118 spatiotemporal variation in shade). We determined spatial variation in drought by measuring a
119 detailed spatial gradient of soil water potential at the seedling sites (i.e. spatial drought) and
120 temporal variation in drought by determining dry season severity (inter-annual drought). We then
121 correlated shade responses to drought responses for growth, survival and, finally, growth versus
122 survival.

123 We hypothesise that there is an interspecific trade-off (i.e. a negative correlation)
124 between performance in shade versus drought, because we expect a trade-off in plant adaptations
125 to cope with shade and drought[9-10]. Additionally, we expect higher light availability in drier
126 habitats and during droughts (and vice versa)[20-23,30,31], allowing species to be adapted to either
127 shade or drought because they would temporarily be released from the other stress. In order to
128 understand how performance of species in shade and drought is linked to broader demographic
129 strategies, we related shade and drought responses to an independently assessed fast-slow
130 continuum based on demographic rates (recruitment, growth and survival) ranging from
131 conservative to acquisitive species[16]. On BCI, conservative species with slower growth and
132 lower mortality have traits that confer shade tolerance, such as high wood density[33]. Thus, we
133 hypothesize that more conservative species perform better in the shade than acquisitive species.
134 On the other hand, acquisitive species should cope better with drought, based on the expected
135 trade-off between shade and drought responses (see above).

136 **Results**

137 *Responses to shade and drought*

138 Ninety-one species fulfilled the sample size requirements for growth and/or survival analyses.
139 For growth, we estimated shade responses for 63 species and spatial and inter-annual drought
140 responses for 84 species (62,973 observations in total). For survival, we estimated shade and
141 drought responses for 27 and 45 species, respectively (31,560 observations in total). Fewer
142 species fulfilled sample size requirements for analyses of light responses because the canopy
143 measurements used to estimate light availability took place in 12 of 20 years[34].

144 There was at least one significant growth or survival response to shade or drought for
145 31% of the species included in the analyses (28 of 91 of species, Supplementary Table S1-S2,
146 Fig. S1). Figure 1 illustrates shade and drought responses of growth and survival for *Faramea*
147 *occidentalis*, the most common species in our study, which grew significantly slower in the
148 shade and had lower survival during drought. Most, but not all, of the significant responses to
149 shade or drought were negative, i.e. weaker performance, with increasing shade or drought
150 (Supplementary Table S1.1). As reported earlier from these seedling data[35], relative growth rates
151 decreased and survival increased significantly with height for the large majority of species (86%
152 and 76% of species, respectively, see Supplementary Table S1.1). Explained variance (R^2) was
153 0.24 in the growth model and 0.12 in the survival model.

154 *Relationship between shade and drought responses*

155 There was a trade-off (i.e. a significant negative correlation) between growth responses to shade
156 and survival responses to inter-annual drought ($\beta_{1,gr} \sim \beta_{3,su}$, Fig. 2b) and between survival
157 responses to shade and inter-annual drought ($\beta_{1,su} \sim \beta_{3,su}$, Fig. 2d). There was also a marginally
158 significant negative correlation between growth responses to shade and inter-annual drought
159 ($\beta_{1,gr} \sim \beta_{3,gr}$, Fig. 2a). Survival responses to shade and growth responses to inter-annual drought
160 were unrelated ($\beta_{1,su} \sim \beta_{3,gr}$, Fig. 2c). Results were robust when we included individuals that
161 resprouted, were visually damaged or infected by pathogens (Supplementary Fig. S1.1). We
162 found no significant relationships between responses to shade and spatial drought ($\beta_{1,su} \sim \beta_{2,gr}$,
163 Supplementary Fig. S1.2).

(8)

Responses in relation to the fast-slow continuum

Survival responses to inter-annual drought (β_3) increased with species' scores on the fast-slow continuum, with scores on the fast-slow continuum from an independent analysis of the performance of trees ≥ 1 cm dbh in the 50-ha plot[33]. Species at the fast end of the fast-slow continuum (low PCA score, fast-growing species with low survival rates) suffered large reductions in survival in years with severe dry seasons, while species at the slow end of the continuum had little reduction in survival (Fig. 3d). In contrast, other responses (growth to inter-annual drought, and growth or survival to shade or spatial drought) were unrelated to the fast-slow continuum (Fig. 3a-c, Supplementary Fig. S1.3). These results were robust when the fast-slow continuum was calculated with seedling growth and survival in addition to performance of trees ≥ 1 cm dbh and with additionally including seed number and seedling recruitment (Supplementary Table S1.2).

Discussion

We assessed the interspecific relationship of species responses to shade and drought in a naturally regenerating tropical seedling community. We found relatively few significant responses of species to shade or drought (Supplementary Table S1.1), in part because many species had modest sample sizes and were limited to part of the observed shade and drought gradients. Yet, there was an interspecific trade-off in responses to shade and dry season severity (Fig. 2), indicating that the ability to cope with (or perform better under) shade or drought comes at the expense of coping with the other stress. Weaker performance during severe dry seasons was also related to a faster demographic strategy (Fig. 3d). Future increases in drought length or severity may come with decreases in shade intensity, which would reinforce a shift towards more drought tolerant and less shade tolerant species.

(9)

Responses to shade and drought

The proportion of species responding significantly to shade or drought was relatively low (Supplementary Table S1.1), which contrasts with reported seedling sensitivity to shade and drought (e.g. [36-38]). This is likely caused by high uncertainty in responses for the many species with low sample sizes, decreasing the chance of finding significant responses for these rare species (Supplementary Fig. S1.4). In addition, many rare species that we could not include are habitat specialists that likely respond more strongly to shade or drought. Second, dispersal or recruitment limitation curtail seedling distributions along light and moisture gradients to sites near successful adults. Seeds of moisture sensitive species rarely disperse to dry microsites[39,40], and if they do and they germinate, many seedlings die during dry spells before inclusion in the annual census[41]. Likewise, seeds of light-demanding species fail to germinate in low light[42]. There were particularly few significant responses to spatial drought. This is likely due to the relatively shallow gradient in spatial drought in the 50-ha plot[35], particularly when compared to other tropical forests[43]. Finally, there may be fewer significant responses to shade than expected because our shade index could not capture ephemeral sunflecks, which are important sources of light for understory plants[44,45].

Unexpectedly, some species performed better in shade or drought (Supplementary Table S1.1). Species may have directly suffered from excessive light (photoinhibition) or water (waterlogging)[46,47]. Alternatively, shade may reduce drought stress, especially during severe dry seasons[48-50]. There was a negative correlation across the 200 seedling census sites between our indices of shade and spatial drought (Supplementary Fig. S1.5, $r = -0.26$, $p < 0.001$), which is consistent with this possibility. Additionally, shade or spatial drought may release seedlings from other stresses. Shade may release seedlings from strong competition for space in gaps[51]. Drought

210 may release seedlings from pathogens[52] or damage from overland water flow on wet slopes
211 during heavy rains[53]. In sum, the positive responses of some species to shade and drought
212 highlight that species responses are not strictly synonymous with shade or drought tolerance. We
213 studied natural variation in shade and drought conditions that incorporate various other biotic
214 and abiotic influences on plants[11,54]. Thus, our approach allows for a more holistic understanding
215 of the ecological mechanisms that affect seedling performance under natural shade and drought
216 conditions, where their relevance should emerge.

217 *Trade-off between shade and drought responses*

218 As expected, we found an interspecific trade-off between responses of species to shade and inter-
219 annual drought; species that performed worse in the shade were not affected (or even performed
220 better) during intense dry seasons and vice versa (Figs. 2a, b and d). The trade-off between shade
221 and inter-annual drought resulted from the relative lack of doubly poorly adapted species and
222 'superspecies'. Relatively few species performed worse in both shade and drought (i.e. bottom-
223 left quadrants of Figs. 2a, b and d). Such species would be outcompeted by species that are well-
224 adapted to shade or drought, and hence would be unlikely to persist in the local community[6,55]. In
225 contrast, although some species performed better in either shade or drought, no species
226 performed better in both (i.e., top-right quadrants of Fig. 2a, b and d). Such species would be
227 akin to 'superspecies' (cf. Tilman[6]) that would dominate the community. However, many of the
228 species in our study had responses that deviated considerably from the trade-off relationship,
229 indicating that the trade-off is not absolute[10,11].

230 Correlations between environmental conditions likely also contributed to the trade-off
231 between responses to shade and inter-annual drought. Species that performed worse in the shade
232 sometimes benefitted during severe dry seasons (bottom-right quadrant of Fig. 2). Reduced cloud

233 cover and increased solar irradiance during severe dry seasons[30,31] might contribute to this effect.
234 Conversely, species that performed worse in years with severe dry seasons tended to have
235 slightly (and sometimes significantly) better performance in the shade (top-left quadrants of Fig.
236 2 a-d). The negative correlation between spatial variation in light and drought (Supplementary
237 Fig. S1.5) might also contribute, with drought-sensitive species protected during drought by
238 wetter conditions in the shade. In sum, the temporary release from shade during drought and
239 from drought pressure in shaded sites may have constrained the evolution of combined tolerance
240 to shade and drought [8].

241 The mechanisms leading to the observed trade-off remain unknown. Experiments found
242 interspecific trade-offs in seedling traits that may underlie a trade-off in species performance in
243 shade versus drought[24,56,57]. For example, there was a trade-off in biomass allocation to leaves
244 and roots[24] as proposed by Smith and Huston[9]. However, low biomass allocation to leaves or
245 roots does not preclude tolerance to shade or drought. For example, shade tolerant species can
246 compensate for low aboveground biomass allocation by producing thinner leaves or reducing
247 growth rates[13]. Other adaptations increase both shade and drought tolerance, including high
248 wood and vessel density[16]. Still other traits increase shade or drought tolerance, but the effect of
249 a trait that increases shade tolerance on drought tolerance and vice versa is unknown. For
250 example, investment in carbohydrate storage and defence against herbivores and pathogens are
251 associated with high seedling survival in the shade[5,58,59]. As another example, species may avoid
252 drought through deciduousness[13,24]. These adaptations have metabolic costs [60-62] and could
253 contribute to the trade-off in shade and drought responses.

Relationship between shade and drought responses and the fast-slow continuum

We hypothesised that responses to shade would correlate with the fast-slow continuum, which was not the case (Fig. 3a-b). This is surprising given the abundant evidence that fast species (with high growth and low survival rates) tend to be light-demanding, while slow species (with high survival and low growth rates) tend to be shade tolerant (e.g. [63,64]). As discussed previously, our ability to detect interspecific variation in shade responses is limited because the most light-demanding species were generally too rare to be included in our analyses (i.e. the paucity of species on the left side of Figs. 4a, b). In addition, species may respond differently to shade in terms of height growth versus diameter growth, for example if seedlings prioritize height growth until they capture enough light for diameter growth as saplings[65]. Species may also undergo ontogenetic shifts in shade tolerance[66], although such ontogenetic shifts have proven to be very rare among species present in the BCI 50-ha plot[67-69].

Species with a slow demographic strategy were more tolerant to severe dry seasons in terms of survival than species with a fast strategy (Fig. 3d). This is likely due to the high cost of drought adaptations (see *Discussion: Trade-off between shade and drought responses*). We did not expect a conservative strategy of drought-tolerant species, because we hypothesised that slow species would be shade tolerant and that shade and drought responses traded off. Yet, similar results have been found in northern hemisphere species that exhibited a trade-off in shade and drought tolerance; drought tolerance corresponded with conservative traits (long leaf life span and high leaf dry mass), while shade tolerance did not correlate with a fast-slow continuum because it involved both conservative (long leaf life span) and acquisitive (low leaf dry mass) traits[70]. Trait comparisons of the slow and fast species in our study can help to understand

whether shade or drought tolerance affects the position of species on the fast-slow continuum most.

Implications of the trade-off between shade and inter-annual drought tolerances

The trade-off between responses to shade and drought may have significant consequences for the future dynamics of tropical forests. As the climate changes, droughts are becoming more frequent and severe[71], which is expected to cause a shift in species composition to species that perform better during drought[72,73]. As tropical forests receive more solar radiation during droughts[30,31], species performing well during drought would be released from shaded conditions. Thus, the drought-shade trade-off could reinforce a shift to more drought-adapted and less shade-adapted species as observed in Ghana[74,75].

It remains unclear how the trade-off may interact with other factors that may cause performance differences among species (e.g. nutrient availability or pest pressure). Evaluating trade-offs among responses to multiple stresses simultaneously can significantly improve our understanding of life-history strategies of species[33]. Thus, a next step would be to evaluate if responses of species to shade and drought are related to their responses to other factors, or if the latter responses form independent dimensions of species strategies in coping with multiple stresses.

Methods

Study site

We conducted this study in old-growth, lowland, moist tropical forest in the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama (9.15° N, 79.85° W). Annual rainfall averages 2660 mm, with a pronounced dry season from mid-December until early May[76].

298 Approximately 10% of the crown area in the plot is deciduous during the dry season[77]. Severe
299 dry seasons tend to occur during El Niño events, when the dry season generally starts early and
300 ends late[31,78]. Soil water availability varies spatially with topography in the plot, with plateaus
301 generally being drier than slopes[79,80].

302 *Seedling censuses*

303 We monitored height growth along the main stem and survival annually from 1994 to 2014 for
304 all seedlings (no minimum size) at 200 permanent seedling census sites (see [81] for details). Each
305 site included three 1-m^2 seedling plots (see [82] for methods). The sites are situated along 2.7 km of
306 trails in the 50-ha plot and cover all topographic habitats (cf. [83]) except stream sides. We
307 excluded individuals that had resprouted or were visually damaged or infected by pathogens
308 because this damage likely had a larger effect on performance than variation in shade or drought.
309 We also excluded growth for individuals that were more than 200 cm tall, as their height was
310 measured inaccurately. Finally, we excluded observations for census intervals that deviated more
311 than 30 days from a full year.

312 *Quantification of shade and drought*

313 We quantified shade intensity for all 200 sites using a shade index based on annual canopy
314 censuses conducted in 12 years (1995-1996 and 2003-2012, data from Condit[34]). The canopy
315 censuses were conducted on a 5m grid across the 50-ha plot[84]. In each grid cell, presence or
316 absence of vegetation was recorded with an ocular range finder in six height intervals: 0-2 m, 2-5
317 m, 5-10 m, 10-20 m, 20-30 m and ≥30 m. We assumed that vegetation casts shade as a 5m
318 diameter circle at the average height of the intervals (at 35m height for the highest interval). We
319 estimated the amount of shade cast in the understory (at 0.5 m height) using Beer's law (i.e. a

(15)

constant proportion of light removed by each layer present) and trigonometry (i.e. the angle of sky overshadowed by vegetation, see Rüger *et al.*[84] for more details). The relative shade index (S) ranged from 109 to 218 (unitless, mean = 169, SD = 23) with increasing values representing deeper shade, i.e. lower light availability.

We quantified dry season intensity using the maximum cumulative water deficit (MCWD) of the dry season preceding the growth or survival observations (1994-2013, published in Condit *et al.*[85]). MCWD is the best predictor of species distributions along a regional rainfall gradient in Central Panama and strongly affects tree growth and mortality on BCI[85,86]. To derive MCWD, we calculated a daily water balance as rainfall minus potential evapotranspiration (PET). We used daily rainfall records from BCI and the average daily PET on BCI from the period 1994-2007, which we assumed to hold across years[85]. We summed daily balances for every possible set of consecutive days between 1 September and 1 July of the next year (encompassing one dry season). The most negative value, i.e. the extreme deficit equalled the MCWD of that year. MCWD ranged from -618 to -328 mm in the years with the most and least severe dry seasons, respectively (mean = -464 mm, SD = 95 mm). We multiplied MCWD by -1 so that larger values correspond to more severe drought. This index of dry season intensity (D_I) captures inter-annual drought variation.

To quantify spatial drought variation, we measured dry season soil water potential (SWP) at the 200 seedling census sites at 15 cm depth (WP4C Dewpoint PotentiaMeter, Decagon Devices, Inc, Pullman WA, USA). As rooting depth of the seedlings was unknown, we took additional samples at 40 and 100 cm depth at 36 seedling sites and 66 sites along the border of the 50-ha plot, and confirmed that SWP at 15, 40 and 100 cm depth were positively correlated ($p < 0.001$, Supplementary Fig. S1.6). We completed SWP measurements three times in a moderate

dry season (February, March and April 2015) and once in a severe dry season (March 2016). The latter dry season occurred during the 2015-16 El Niño event and was the third longest dry season recorded on BCI since 1954[76]. We excluded samples taken after a rain in April 2015, and outliers identified using soil water retention curves for a subsample of sites (see Supplementary Information and Fig. S2.1 for details). SWP measurements taken at the same sites were positively correlated among all four sampling rounds, indicating that spatial differences in SWP were consistent over time ($p < 0.001$, Supplementary Fig. S1.7). We calculated the median SWP per site across the four sampling periods to quantify spatial variation in water availability. The median SWP across the 200 sites ranged from -1.57 to 0.00 MPa at the driest and wettest site, respectively (mean = -0.39 MPa, SD = 0.27 MPa). We multiplied median SWP by -1 so that again larger values corresponded to drier conditions for our spatial drought index (D_S).

Estimating shade and drought responses

We analysed annual relative height growth rates (RGR), because it decreased monotonically with seedling height whereas absolute height growth varied nonlinearly with height. We calculated RGR as:

$$\mathrm{RGR} = \frac{\ln(\mathrm{height}_2) - \ln(\mathrm{height}_1)}{t_2 - t_1} \qquad (1)$$

where height_2 and height_1 are the height measurements at times t_2 and t_1, respectively. As RGR was strongly right-skewed and contained negative values (preventing the use of a log transformation), we transformed RGR using a modulus transformation[87]:

$$\mathrm{RGR}_t(\lambda) = \begin{cases} \mathrm{RGR}^{\lambda} & \mathrm{RGR} \geq 0 \\ -\{(-\mathrm{RGR})^{\lambda}\} & \mathrm{RGR} < 0 \end{cases} \qquad (2)$$

where RGR_t is the transformed RGR. This transformation effectively reduced skewness with λ values between 0.3 and 0.6 in a recent study of diameter growth of saplings and trees in the BCI 50-ha plot[85]. We used $\lambda = 0.6$, as this reduced skewness most effectively (i.e. it resulted in the smallest difference between median and mean RGR). Additionally, we excluded extreme RGR outliers using a modified z-score. This scores indicates outliers using the distance of an observation from the median, divided by the median absolute deviation of all observations from the median (see Iglewicz and Hoaglin[88] for details). We quantified first-year survival for the year after a seedling was first recorded, discarding all seedlings present in the initial 1994 census because their ages are unknown.

We used a Bayesian approach to quantify species growth and survival responses to shade and drought. We modelled the transformed RGR_t of individual i of species j in site s and year y ($G_{i,j,s,y}$) (cm cm^{-1} year^{-1}) using a normal distribution with predicted growth $g_{i,j,s,y}$ and standard deviation σ_j:

$$G_{i,j,s,y} \sim \text{normal}(g_{i,j,s,y}, \sigma_j) \quad (3)$$

Independent variables were the shade ($S_{s,y}$), spatial drought ($D_{S,s}$) and inter-annual drought ($D_{I,y}$) indices for site s and year y and seedling height (cm) of individual i at the beginning of the census interval in year y ($H_{i,y}$):

$$g_{i,j,s,y} = \beta_{0,j} + \beta_{1,j} \times S_{s,y} + \beta_{2,j} \times D_{S,s} + \beta_{3,j} \times D_{I,y} + \beta_{4,j} \times \ln(H_{i,y}) + u_i + u_s + u_y \quad (4)$$

where the species-specific coefficients describe the mean RGR_t ($\beta_{0,j}$), the responses to shade ($\beta_{1,j}$), spatial drought ($\beta_{2,j}$) and inter-annual drought ($\beta_{3,j}$) and the effect of height ($\beta_{4,j}$). We did not impose hyperdistributions on the β parameters to prevent the abundant species from dominating the results. We included random effects for individual (u_i), site (u_s) and year (u_y). We

385 tested for an interaction between responses to shade and spatial drought ($\beta_{5,j} \times S_{s,y} \times D_{S,s}$) and
386 between responses to shade and inter-annual drought ($\beta_{6,j} \times S_{s,y} \times D_{S,s}$), but we found few
387 significant positive or negative interactions per parameter (≤ 5 species).

388 We modelled survival using a Bernoulli distribution in equation (3) and a logistic
389 adaptation of equation (4). The survival model did not include a random effect for individual
390 because we evaluated survival once per individual. As we did not have prior information, we
391 used flat (non-informative) priors. We fitted models with the Bayesian inference software
392 package RStan version 2.16.2[89]. The Supplementary Information includes the Stan code,
393 implementation procedures and model diagnostics.

394 For both models, the shade ($\beta_{1,j}$) and drought responses ($\beta_{2,j}$, and $\beta_{3,j}$) represent the slope
395 of the relationship between performance (growth or survival) and S, D_S and D_I, respectively.
396 Species performed significantly worse (negative slope) or better (positive slope) in higher shade
397 or drought when the 95% credible interval (CI) excluded 0. We analysed responses for all
398 freestanding, woody species that were abundant enough to estimate reliable parameter values.
399 We included species with ≥ 50 growth observations or ≥ 100 survival observations over the 12
400 years with canopy censuses to quantify shade responses and over all 20 years to quantify drought
401 responses. For the eight years lacking canopy measurements, we estimated growth or survival
402 responses to drought only by removing the shade response term ($\beta_{1,j} \times S_{s,y}$) from equation (4) (see
403 model code in Supplementary Information for details). We assessed the overall predictive power
404 of the growth and survival models by calculating the proportion of explained variance (R^2)
405 following Gelman and Hill[90].

(19)

406 *Testing the relationship between responses*

407 We tested the relationships of species-specific responses to shade (β_1) versus spatial (β_2) and
408 inter-annual drought (β_3) using weighted Pearson correlations. We evaluated correlations for
409 growth responses, survival responses and growth versus survival responses. For each species j
410 and parameter p, we used the 95% credible interval of $\beta_{p,j}$ ($CI_{p,j}$) as a weight ($\text{weight}_{p,j}$) as
411 follows:

412 $$\text{weight}_{p,j} = 1 - \frac{\text{CI}_{p,j}}{\max(\text{CI}_p)} \qquad (5)$$

413 The species with the widest $\text{CI}_{p,j}$ (i.e. largest uncertainty) had weight zero, which we reset to half
414 the weight of the species with the second widest $\text{CI}_{p,j}$. As the weighted correlations required one
415 weight per species, we used the mean of the weights of their respective shade ($\beta_{1,j}$) and spatial
416 (β_2) or inter-annual drought response ($\beta_{3,j}$).

417 *Relating responses to the fast-slow continuum*

418 To test whether responses to shade and drought were related to demographic strategies, we
419 evaluated relationships between responses to shade (β_1), spatial drought (β_2) or inter-annual
420 drought (β_3) and species positions along an independently quantified fast-slow continuum[33]. A
421 low score on the first principal component axis of Rüger et al. (2018) corresponds to species with
422 fast growth and low survival (i.e. fast species), and a high score corresponds to species with slow
423 growth and high survival (i.e. slow species). We evaluated these relationships using weighted
424 Pearson correlations as described above (see *Methods: Testing the relationship between*
425 *responses*).We conducted all analyses in R version 3.4.1[91].

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Competing interests

The authors declare no competing interests.

Acknowledgements

S.J.K., N.R. and C.W. acknowledge the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – FZT 118. This project has been conducted in the framework of the iDiv-Flexpool – the internal funding mechanism of iDiv. S.J.K. was supported through a Short Term Fellowship of the Smithsonian Tropical Research Institute (STRI). N.R. was funded by a research grant from the DFG (RU 1536/3-1). We thank Anke Hildebrandt and yDiv (the graduate school of iDiv) for advice, the STRI staff that facilitated the project, the field assistants that collected data and Lourens Poorter for constructive comments.

Author Contributions

S.J.K., B.M.J.E, N.R. and C.W. conceived the study. S.J.W. and A.H. designed and performed the seedling censuses. S.J.K. collected the soil moisture samples, analysed the data and led the writing of the manuscript with substantial contributions from all authors.

Data Availability

Seedling and inter-annual drought data are available on request via ForestGEO[81] and Condit *et al.*[85], respectively. Shade and soil water potential data are available from Condit[34] and Kupers *et al.*[92], respectively.

446 **Tables**

447 Table 1 Studies that tested the interspecific relationship between tolerances to shade and drought.

Study	Vegetation type	Life stage	Nr. spp.	Approach	Shade tolerance definition	Drought tolerance definition	Support for hypothesis*
Suding *et al.*[57]	Lake-plain prairie	Seedlings	11	Experimental performance	Growth in low versus high light	Growth in low versus high soil moisture	Trade-off†
Niinemets and Valladares[10]	Temperate forest	Seedlings and saplings	806	Species distributions / traits	Subjective species occurrence indices compiled across sources	Subjective species occurrence indices compiled across sources	Trade-off
Stahl *et al.*[93]	Temperate forest	Seedlings and saplings	305	Species distributions / traits	Subjective species occurrence indices compiled across sources	Subjective species occurrence indices compiled across sources	Trade-off†
Poorter and Markesteijn[24]	Tropical dry and moist forest	Seedlings	38	Species distributions	Juvenile crown exposure	Relative abundance of species in dry versus moist forest site	Trade-off

Brenes-Arguedas *et al.*[56]	Tropical moist forest	Seedlings	24	Experimental performance	Leaf area growth in the understory	Survival in control versus irrigated conditions	Trade-off‡
Martínez-Tillería *et al.*[94]	Arid scrubland	Seedlings	6	Experimental performance	Growth and survival in low, medium and high light	Growth and survival in control versus irrigated conditions	Independence†
Sack and Grubb[14]	Temperate forest	Seedlings	4	Experimental performance	Growth in high versus low light treatment	Growth in high versus low watering treatment	Independence†
Sack[11]	Temperate forest	Seedlings	13	Experimental performance	Growth and survival in high versus low light treatment	Growth and survival in high versus low watering treatment	Independence
Sánchez-Gómez *et al.*[12]	Mediterranean forest	Seedlings	8	Experimental performance	Growth in high versus low light treatment	Growth in high versus low watering treatment	Independence
Markesteijn and Poorter[13]	Tropical dry and moist forest	Seedlings	62	Species distributions	Juvenile crown exposure	Relative abundance of species in dry versus moist forests	Independence

Engelbrecht *et al.*[95]	Tropical moist forest	Seedlings and adult trees	28	Species distributions / Experimental performance	Percentage of recruits in high light conditions	Species distributions along rainfall and soil moisture gradients, survival in dry versus irrigated conditions	Independence
Sterck *et al.*[25]	Tropical dry forest	Saplings	13	Model parametrized with functional traits	Simulated light compensation point	Simulated water compensation point	Acquisitive vs. conservative‡
Sterck *et al.*[96]	Tropical dry forest	Saplings	37	Model parametrized with functional traits	Simulated light compensation point	Simulated water compensation point	Acquisitive vs. conservative‡
Markesteijn *et al.*[26]	Tropical dry forest	Seedlings	40	Species distributions, functional traits	Juvenile crown exposure	Midday leaf water potential	Acquisitive vs. conservative

Ouédraogo *et al.*[97]	Tropical moist forest	Trees ≥ 10 cm dbh	229	Field performance / species guilds	Maximum growth rate and regeneration guild	Growth responses to climatological drought and modelled soil water content	Acquisitive vs. conservative†

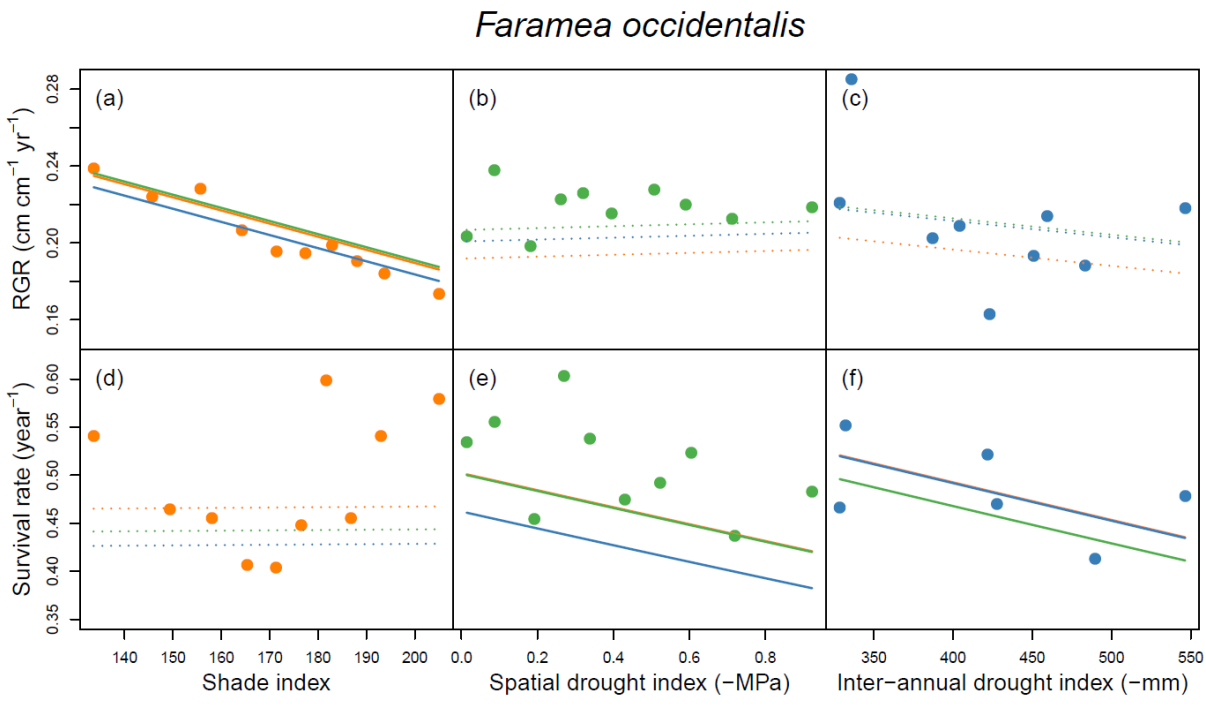
448 * Support for the 'trade-off' or 'acquisitive versus' conservative hypothesis was found when a correlation between tolerances was significantly
449 negative or positive, respectively ($p < 0.05$), and support for the 'independence' hypothesis was found when the correlation was not significant.

450 † Relationship between tolerances was evaluated other than through a correlation between tolerances, e.g. through relating shade and drought
451 tolerance to a principle coordinate analysis of functional traits, comparison of performance of individual species/guilds among treatments, or
452 among natural conditions varying in shade or drought intensity.

453 ‡ Hypothesis was partly supported, correlation between shade and drought tolerance was marginally significant ($0.05 \leq p < 0.10$).

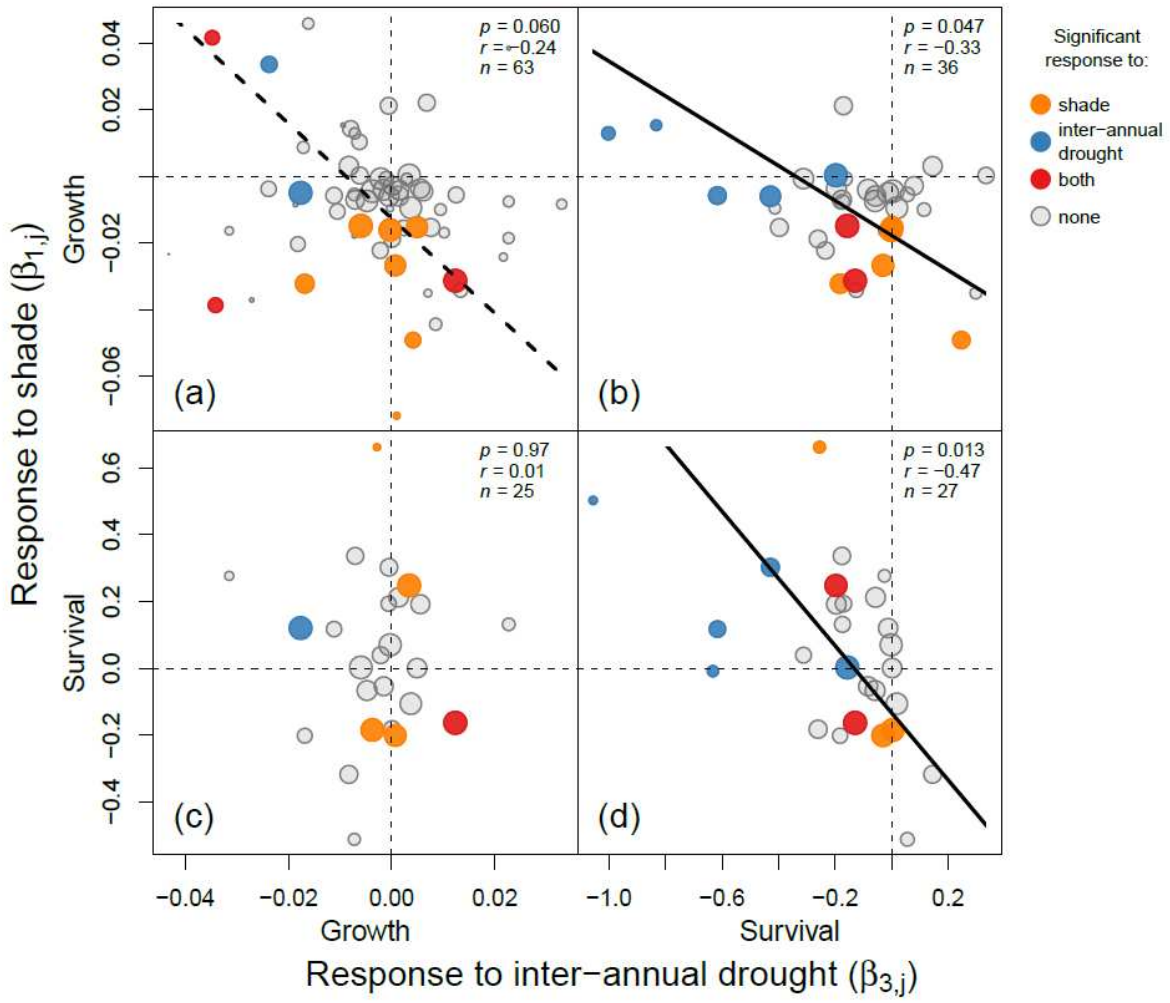
Figures

Figure 1 Relationship between observed and fitted relative growth rate (RGR, upper panels) and survival rate (lower panels) and shade (a,d), spatial drought (b,e) and inter-annual drought (c,f) of the abundant treelet *Faramea occidentalis*. Growth decreased significantly in deeper shade (a) and survival decreased significantly in drier sites (e, spatial drought) and years (f, inter-annual drought). Large dots represent mean observed growth or survival for ten shade or drought classes, each containing 10% of the individuals of the species (only six classes in (f), due to high abundance in one year). Lines show fitted growth and survival with increasing shade (a,d, orange), spatial drought (b,e, green) and inter-annual drought (c,f, blue), at mean values of the other independent variables. Solid and dotted lines indicate significant and non-significant responses, respectively. Lines whose colour differs from the large dots within each panel represent 1 SD increase in shade (orange), spatial drought (green) or inter-annual drought (blue). Figure S1 presents responses to shade and drought for all analysed species.



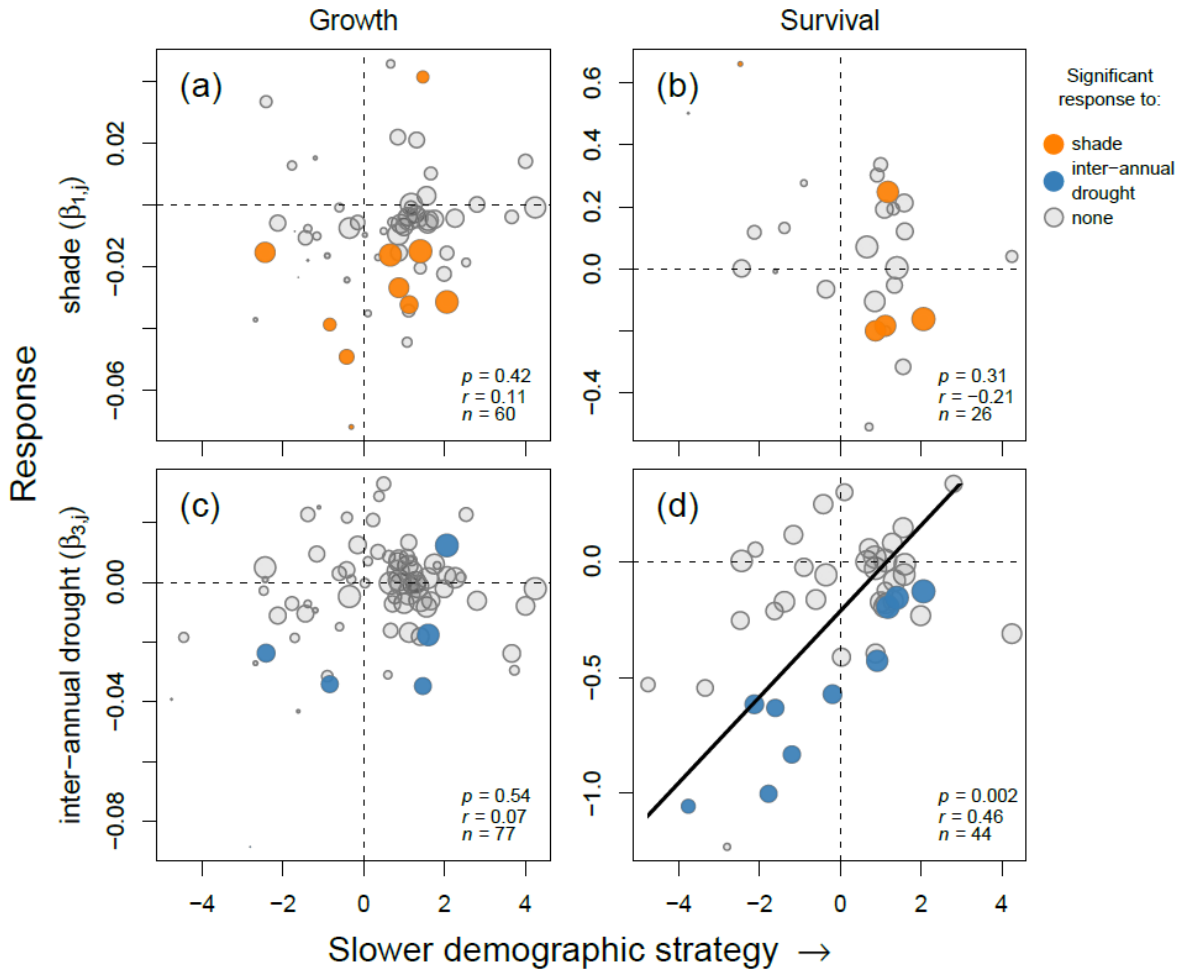
(26)

Figure 2 Relationships between species responses to shade and inter-annual drought (i.e. dry season severity) for growth (a), survival (d), or growth versus survival (b,c). Solid and dashed lines indicate significant ($p < 0.05$) and marginally significant ($0.05 \leq p < 0.10$) relationships, respectively. Negative relationships indicate a trade-off between shade and drought responses. Correlations are weighted by the uncertainty in species tolerances (smaller dots have higher uncertainty and lower weight, see equation (5) in text). Colours identify species with insignificant (grey) or significant responses to shade (orange), inter-annual drought (blue) or both (red).



(27)

Figure 3 Relationships between the fast-slow continuum and responses to shade (a,b) and dry season severity (i.e. inter-annual drought) (c,d) for growth (left) and survival (right). The position of species along the continuum was quantified by a weighted PCA of demographic rates (growth, survival, number of sapling recruits) of trees ≥ 1 cm dbh recorded in the BCI 50-ha plot[33]. Low and high scores correspond to species with fast and slow demographic strategies, respectively. Colours identify species with insignificant (grey) or significant responses to shade (orange) or inter-annual drought (blue). Relationships were consistent when the fast-slow continuum was calculated using seedling performance and/or seed number additionally (see Supplementary Table S1.2).



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4. GENERAL DISCUSSION

In this dissertation I measured soil moisture in two dry seasons across 363 sampling sites in the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama. No previous study has provided soil moisture measurements with such high spatial and temporal resolution within a tropical forest. I used these data to map soil moisture across the 50-ha plot (Paper 1), study the demographic mechanism by which soil moisture affects species distributions (Paper 2) and compare the effect of spatial variation in soil moisture with inter-annual variation in droughts and spatiotemporal variation in light availability (Paper 3). In this discussion, I synthesise the findings of my work to evaluate the effect of soil moisture in shaping tropical forest tree species communities and I provide an outlook for possible future studies that can build on my findings.

4.1 Soil water availability and drought stress for plants

Before discussing the observed species responses to my soil moisture measurements, it is important to determine if (and to what extent) the soil moisture levels I measured are low enough to cause drought stress and limit plant performance. Drought limits plant performance by causing cell turgor loss; consequently, drought tolerance in plants is best quantified in terms of the leaf water potential at turgor loss (Bartlett et al. 2012). Plants need to maintain leaf water potential lower than soil water potential (SWP) to maintain water flow the soil, i.e. to avoid hydraulic failure (see Fig. 2). I compare various tropical forests in terms of their SWP minima, which indicate the most stressful drought conditions plants face. Minimum SWP is relevant for causing hydraulic failure, which can cause plant mortality (Sperry et al. 2002, McDowell et al. 2008). Carbon starvation can also cause mortality when plants close their stomata during prolonged droughts to avoid hydraulic failure (McDowell et al. 2008, McDowell 2011). Most studies that measured SWP in the tropics did so at very few locations, but generally with sensors that provide a time series across wet and dry seasons, which would allow determining drought duration. I do not have continuous measurements of SWP throughout the dry season, so from my SWP data it is not feasible to accurately determine the amount of time and level of soil drought needed to cause carbon starvation.

The lowest SWP I measured in the 50-ha plot (−2.45 MPa) was similar to the lowest SWP measured in the plot in the relatively strong dry season of 1985 (Table 1). As expected (see section

1.2), SWP was lower in late dry season conditions and during the El Niño drought, as well as on flatter areas (Paper 1). Minimum SWP was much lower in the 50-ha plot compared to the mild 1999 dry season in the Lutz catchment on BCI, located 1.25 km from the 50-ha plot (Table 1). SWP was likely higher in the Lutz catchment because it has much steeper slopes than the 50-ha plot, which are generally wetter than flatter areas (Paper 1, Becker et al. 1988, Daws et al. 2002). My minimum SWP was similar to minima measured at Pipeline Road (−2.1 MPa) close to BCI (Santiago et al. 2004) and in the moist forest of La Chonta in Bolivia (Table 1). The dry season is longer in Bolivia, but I measured SWP during a strong El Niño drought while La Chonta had erratic rainfall in the dry season in which SWP was measured (Markesteijn et al. 2010). SWP was slightly higher than in a moist forest in Ghana. The Ghanaian forest has a dry season of similar length to BCI (Table 1), but experienced a strong dry season during SWP measurements. Both forest have much lower total annual rainfall than BCI (Table 1). SWP is considerably lower in seasonal moist than in aseasonal rainforests in Malaysia, where it rarely drops below −1 MPa, even though these aseasonal forests had similar annual rainfall (Table 1). Thus, the length and intensity of the dry season appear to be more important for determining soil drought than annual rainfall.

Table 1 Minimum soil water potential (SWP) measured in tropical forest sites with varying climate regimes.

Site	Annual rainfall (mm)	Dry season length (months)	Minimum SWP (MPa)	Reference
50-ha Forest Dynamics Plot, Barro Colorado Island, Panama	2660	4	−2.45	Kupers et al. (2019)
50-ha Forest Dynamics Plot, Barro Colorado Island, Panama	2660	4	−2.3	Becker et al. (1988)
Lutz Catchment, Barro Colorado Island, Panama	2660	4	−0.55	Daws et al. (2002)
Central Panama[1]	1800 to 3500	4 to 2	−3.7 to −0.9	Santiago et al. (2004)
Tinte Bepo Forest Reserve, Ghana	1280	4 (+2) [2]	−3.0	Veenendaal et al. (1996)
Inpa / La Chonta, Bolivia[3]	1160 / 1580	6	−7.0 / −2.5	Markesteijn et al. (2010)
Danum Valley Conservation Area, Malaysia	2670	0 [4]	−0.7	Gibbons and Newbery (2003)
Lambir Hills National Park, Malaysia	2700	0 [4]	−0.8	Aiba and Nakashizuka (2007)

[1] Shown is the range of SWP values that this study measured from the dry to the wet side of the rainfall gradient in Central Panama. SWP at the closest site to BCI (Pipeline Road) was -2.1 MPa.

[2] This forest has one strong dry season of 4 months and a milder dry season of 2 months.

[3] Shown are the values for the dry forest (Inpa) and the moist forest (La Chonta).

[4] These forests do not have a distinct dry season, but are subject to occasional (El Niño) droughts.

Minimum SWP becomes relevant if it forces leaf water potential to drop to a level at which turgor is lost (i.e. plants start to wilt) and plant performance is impacted (McDowell et al. 2008, Bartlett et al. 2012). Experiments with up to 28 species from Central Panama show that survival in wet versus dry treatments is correlated with severe wilting, and such wilting occurred in a wide range of leaf water potentials from −2 to −10 MPa, depending on the species (Tyree et al. 2003, Engelbrecht et al. 2007b, Kursar et al. 2009). Only six of these 28 species showed severe wilting above leaf water potentials of −2.45 MPa, the lowest SWP value I measured in the 50-ha plot. Moreover, only two species showed severe wilting above −2 MPa, which constitute most of my SWP measurements (Fig. 13). This indicates that few species would suffer increased mortality at the SWP levels I measured in the 50-ha plot. This may explain why I did not find a link between mortality and species distributions in the plot (see Paper 2 and section 4.2). However, some species had significantly lower survival with decreasing SWP in my study (Paper 2). The naturally regenerating seedlings I studied under the non-manipulated conditions may suffer mortality at higher leaf water potentials, because in contrast to the above experiments they would not be shielded from other pressures that may exacerbate drought stress, such as herbivores (McDowell et al. 2008). Unfortunately, leaf water potentials have not been measured under natural conditions for many tree species on BCI. In the 50-ha plot on BCI, some shrub species reached leaf water potentials of −3 or −4 MPa and showed signs of turgor loss, while deeper rooted shrub species could maintain leaf water potentials at −2 MPa and resisted desiccation (Becker et al. 1988, Tobin et al. 1999).

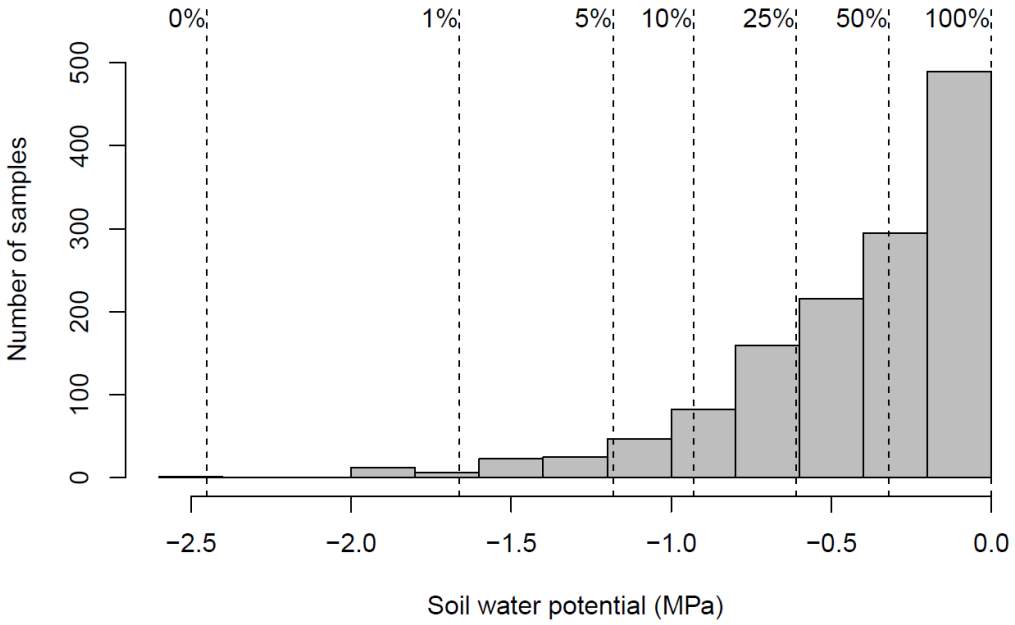

Fig. 13 Histogram of all my soil water potential measurements in the 50-ha plot on BCI. Dashed lines show quantiles of SWP measurements: measurements left of the dashed lines belong to the x^{th} percentage of lowest SWP values.

Growth is likely affected at higher SWP compared to mortality, because 12 of the 28 species (43%) in the experiment mentioned above experienced significantly slower growth in the dry versus the wet treatment, while only 3 species (11%) experienced increased mortality (Engelbrecht and Kursar 2003). Species likely experience reduced growth before severe wilting and mortality occur, because drought leads to a gradual reduction in photosynthesis (Slot and Poorter 2007). Slight wilting occurred at high leaf water potentials (between approximately −0.5 and −1.5 MPa) for all five species in Tyree et al. (2003). Unfortunately, Kursar et al. (2009) did not report SWP at slight wilting for the 28 species in their study. Growth reductions may occur at higher SWP values than mortality, which may explain why we found a significant link between growth (but not mortality) and species distributions in Paper 2 (see section 4.2). Thus, SWP values that I measured in the 50-ha plot on BCI were likely low enough to affect growth of a relatively large number of species, while it may only be low enough to affect mortality of a few species.

4.2 The role of spatial variation in soil moisture in shaping tree species demography and distributions

The first aim of my dissertation was to identify the mechanism by which soil moisture shapes the demography and distributions of tree species within tropical forests. Species demography and distributions have been related to soil moisture in permanent forest plots, but these studies generally used soil moisture measurements at a few locations to contrast habitats with lower and higher soil moisture. On BCI, soil water potential were measured at two locations in the 50-ha plot, which showed that slopes were wetter than plateaus (Becker et al. 1988). These findings were then used to contrast performance and distributions of species on dry plateaus versus wet slopes (Engelbrecht et al. 2007a, Comita and Engelbrecht 2009). The advantage of this approach is that the effect of water availability can be studied with easily accessible topographic data instead of more expensive and labour-intensive soil moisture data.

However, my work in Paper 2 shows that the use of coarse topographic habitats as a proxy for soil moisture measurements can miss important ecological mechanisms. Earlier work on BCI suggested that differences in seedling growth rates of species in dry plateaus versus wet slopes do not contribute substantially to differences in species abundances among habitats (Comita and Engelbrecht 2009). In contrast with these studies, I showed that seedling growth responses to SWP indirectly shaped species distributions along the SWP gradient by influencing seedlings size and thereby mortality rates. In particular, wet-distributed species grew faster on the wet side of the SWP gradient (i.e. they performed ‘best at home’) and they had a home advantage in terms of growth over species from the dry side of the gradient. This allowed the wet-distributed species to escape the vulnerable small size range quicker, reducing their mortality rates and allowing them to become more abundant on the wet side of the gradient over time. I expected that wet-distibuted species would always grow faster than dry-distributed species, because species originating in wet forests on the rainfall gradient in Central Panama grow inherently faster than species originating in dry forests (Brenes-Arguedas et al. 2009, Gaviria et al. 2017). However, wet-distributed species only grew faster than dry distributed species in wet sites. I also expected that dry-distributed species would be more drought tolerant and have lower mortality in drier sites (Brenes-Arguedas et al. 2013). However, dry-distributed species did not have lower mortality on the dry side of the gradient than wet-distributed species, which further supports the mechanism I proposed in Paper

2, i.e. that size dominates mortality for the smallest seedlings and that growth advantages with respect to SWP indirectly shape mortality in later seedling stages.

I also quantified species positions for seedlings along the SWP gradient and compared them to saplings and taller trees, which provided the first evidence that distributions of species along the soil moisture gradient remain constant across life stages. These results extend findings extend from an earlier study in seven tropical forest plots (including BCI), which showed that species composition with respect to continuous variation in topography and soil chemistry remains constant from ≥ 1 cm dbh onwards (Baldeck et al. 2013). In contrast, earlier studies on BCI did not find consistent distributional associations to topographic habitats across life stages and species sometimes even changed preferences to different habitats from the seedling to the adult stage (Comita et al. 2007b). However, topographic habitats vary not just in soil moisture availability but in many more aspects that affect species performance such as disturbance history and pathogen pressure (Comita et al. 2007b), suggesting that other variables in addition to soil moisture influence species associations to topographic habitats. These contrasting findings from topographic habitats and continuous environmental gradients underscore the complexity of species performance in coarse habitats and the need for quantifying species performance on resource gradients such as soil water availability.

My results from Paper 2 show that soil moisture plays an important role in driving the demography and distributions of species, even though few species may show statistically significant demographic responses to or distributional associations with SWP. These findings resolve seemingly contrasting findings in the 50-ha plot. On the one hand, there are relatively few habitat associations of species on BCI, suggesting that habitat specialisation plays only a minor role in maintaining the species diversity in the plot (Harms et al. 2001). A likely reason for this is that topographic heterogeneity on BCI is relatively low compared to other tropical forests and the importance of niche differentiation likely increases with environmental heterogeneity (Brown et al. 2013). Thus, the effect of spatial variation in soil moisture on demography and distributions of species is likely stronger in other tropical forest than on BCI. On the other hand, seedling drought sensitivity of species is significantly related to the position of species on slopes versus plateaus, indicating that soil moisture plays an important role in shaping species composition (Engelbrecht et al. 2007a). In my study there were also relatively few significant demographic responses and

distributional associations to SWP, but the significant relationship between demography and distributions reveals the mechanism that shapes species distributions: species with a growth advantage in wetter sites outgrow the vulnerable small seedling stages quickest, allowing them to escape mortality and become more abundant in wetter sites. Thus, spatial variation in soil moisture shapes species composition and diversity in tropical forests, but detailed SWP measurements are needed to find this mechanism in a forest with relatively homogeneous topography such as on BCI.

Soil water availability also varies vertically with soil depth. On BCI, SWP increases with soil depth in the 50-ha plot (Paper 1). Soil water content increases with depth near the 50-ha plot and stable isotope measurements showed that species vary in the depth at which they take up water (Meinzer et al. 1999). However, there is large variation in water uptake depths related to size differences within and among species, with large trees sourcing water at shallower depths due to their larger root area and greater water storage (Meinzer et al. 1999). Tree species in a seasonal forest in India also partitioned their water uptake at different depths, affecting growth and making species with deeper roots more vulnerable to droughts because their root zones recharged slower with water after drought (Chitra-Tarak et al. 2018). Vertical niche differentiation along water uptake depths is common in various ecosystems (see references in Silvertown et al. 2015). Future studies may use three-dimensional hydrological models to help understand the interaction between horizontal and vertical variation in soil water availability in shaping species performance, distributions and composition in tropical forests.

4.3 Spatial versus inter-annual variation in drought and the roles of light and nutrients in shaping species demography

In Paper 3, I studied seedling growth and survival responses to both spatial variation in drought (the inverse of soil water potential) and inter-annual variation in drought (cumulative water deficit, i.e. dry season severity). Inter-annual drought decreased seedling growth and survival for more species than spatial drought. In contrast, topographic habitats had a stronger effect on the survival of larger seedlings and saplings (≥ 20 cm tall and <1 cm DBH) in the BCI 50-ha plot than dry season severity at the community level (Johnson et al. 2017). Yet, this corroborates my findings in Paper 2, namely that size dominates mortality compared to spatial variation in soil moisture when seedlings are small, whereas growth advantages of species with respect to soil moisture affect mortality for taller seedlings more strongly. Taller seedlings varied more in their survival

responses among species to dry season severity compared to habitats (Johnson et al. 2017). This indicates that drought-sensitive and drought-tolerant species are both exposed to inter-annual droughts (i.e. they cannot escape them spatially), magnifying their different responses as I observed in Paper 3. In contrast, spatial variation in soil moisture excludes drought-sensitive species from dry habitats, decreasing the spatial drought gradient to which these species are exposed and thereby decreasing variation in species responses (see Paper 2 and 3). Thus, while severe inter-annual droughts can strongly limit performance across the species community and across the plot, spatial variation in soil moisture shapes species distributions within the plot. Various other studies confirm the importance of both spatial and temporal variation in drought on seedling performance (Comita and Engelbrecht 2014); for example, seedling survival of species with different distributional associations to soil types that vary in soil moisture was different during a normal year and during slight drought, while survival was equally reduced among habitats and species during a strong drought (Delissio and Primack 2003). Thus, spatial and temporal variation in water availability interact to shape species performance and distributions in tropical forests.

I also quantified growth and survival responses to shade in Paper 3. I found that light affected the growth rates for the largest percentage of species, whereas inter-annual drought affected survival rates for the largest percentage of species (spatial drought had a weaker effect, see section 4.2). However, I cannot draw strong conclusions regarding the relative importance of shade versus drought on seedling performance, because I included different numbers of species for estimating responses to shade and drought; I have shade data for only around half of the census years, so I could not estimate shade responses for rare species which were likely habitat specialists. In addition, the relative importance of shade and drought I found for small seedlings (≥ 0 cm tall) was different from the relative importance for taller seedlings and saplings (≥ 20 cm tall and < 1 cm DBH) in the 50-ha plot: for the latter group, survival was more strongly affected by topographic habitats (a proxy for spatial variation in water availability) than variation in dry season intensity, whereas light plays a relatively minor role (Johnson et al. 2017). Although both shade and drought affect performance of taller trees (≥ 1 cm DBH) on BCI (Condit et al. 1995, Rüger et al. 2011a, Rüger et al. 2011b), their relative importance has not been compared directly. The soil moisture maps I provided in Paper 1 can be used together with shade maps (Condit 2019) to help compare the effects of shade and drought on trees ≥ 1 cm DBH, allowing for a better comparison of their effect across life stages.

The main focus of Paper 3 was to reach the second aim of my dissertation: to determine the relationship between the effects of water and light availability on species demography in a tropical moist forest. As I expected (see section 1.3), there was a consistent trade-off between demographic responses of species to shade and inter-annual drought, indicating that species are either specialized on coping with shade or with drought. This corresponds with an experiment with seedlings from Central Panamanian tree species, in which leaf area growth in the shade traded off with survival in a drought treatment (Brenes-Arguedas et al. 2013). The trade-off emerged from the absence of species that performed particularly well or poorly in both shade and drought (see Fig. 2 in section 3.3). As expected, the trade-off may be reinforced due to higher light availability during droughts, as well as due to higher light availability in drier sites which I found in Paper 3. These findings suggest that a trade-off in shade and drought tolerance applies within tropical moist forests as it does in temperate regions (Niinemets and Valladares 2006, Stahl et al. 2013) and between dry and moist tropical forests (Poorter and Markesteijn 2008).

My findings contrast with evidence for a fast-slow continuum across various biomes, where species with fast growth and low survival are intolerant to shade and drought while species with slow growth and high survival are shade and drought tolerant (Reich 2014). I found that species with better survival during drought (but not shade) fall on the slow side of a fast-slow continuum (i.e. they have slow growth and high survival, see Paper 3), which describes the strongest axis of demographic variation of species in the BCI 50-ha plot (Rüger et al. 2018). Yet, there is abundant evidence that slow tropical forest species are shade tolerant (e.g. Poorter and Bongers 2006, Wright et al. 2010). I discussed various possible explanations for the lack of relationship between shade responses and the fast-slow continuum in Paper 3, the main one being the relative lack of light-demanding species in my study due to small sampling sizes and incomplete shade data, which hampered the comparison of shade responses and the fast-slow continuum. Future studies may relate my shade and drought responses to functional traits to clarify what drives the position of shade and drought tolerant species on the fast-slow continuum, as well as to help understand the mechanisms driving the trade-off between shade and drought responses.

Besides water and light, nutrients also affect tree species communities in tropical moist forests (Vitousek and Sanford 1986). In Central Panama, tree species distributions are strongly related to phosphorus (P) availability (Condit et al. 2013). Soils on BCI are relatively nutrient-rich

and variation in nutrient availability among soil types is relatively low (Yavitt 2000). However, distributions of various species in the 50-ha plot are related to nutrients such as phosphorus, potassium and zinc (John et al. 2007), albeit relatively weakly (Hubbell 2009). Yet, nutrient availability correlates with topography (John et al. 2007) and I showed in Paper 2 that soil moisture correlates with Mg and N availability. This correlation makes it difficult to separate the effect of nutrients and water availability on seedling demography in my models, especially because various species had relatively low sample sizes. Experiments show that species in Central Panama are limited by nutrient availability. Seedling growth on BCI increased with the addition of water as well as a mix of nutrients (Yavitt and Wright 2008). Near BCI, seedling performance increased and biomass allocation to roots decreased with N, K and P fertilisation, indicating a release from nutrient limitation (Santiago et al. 2012, Wurzburger and Wright 2015). However, the effect of spatial variation nutrient availability (i.e. a PCA axis combining many chemical elements) on the mortality of naturally regenerating seedlings in the 50-ha plot is relatively weak compared to topographic habitats that vary in water availability (Johnson et al. 2017). Future studies can compare leaf nutrient concentrations of species (e.g. using data from Schreeg et al. 2013) with species performance and/or distributions on the soil moisture gradient (using SWP maps I provided in Paper 1) and nutrient gradients (using data from John et al. 2007 or Wolf et al. 2015) to disentangle the influence of water and nutrients on species performance and distributions in tropical moist forests.

4.4 Soil moisture niche differentiation and other mechanisms promoting species coexistence in tropical forests

Species coexistence is maintained by stabilising mechanisms, which increase intraspecific relative to interspecific competition (Chesson 2000). The link between demographic responses and species distributions with respect to soil moisture (Paper 2) is an example of spatial niche partitioning with respect to resources. This is a stabilising mechanism that promotes species coexistence, because it increases intraspecific competition due to increased population densities on of species on different parts of the soil moisture gradient (Silvertown et al. 2015). Inter-annual variation in water availability as studied in Paper 3 can also help maintain diversity by providing opportunities for temporal niche differentiation, also known as the storage effect (Silvertown et al. 2015). Temporal niche differentiation with respect to water availability may explain the coexistence of trees and

lianas on BCI, as trees growth faster in the wet season while lianas grow faster in the dry season (Schnitzer and van der Heijden 2019). Other stabilizing mechanisms are interspecific trade-offs in performance with respect to resource use, which increase intraspecific competition as different species are specialised to sustain themselves under low availability of different resources (Chesson 2000). One example is the trade-off I found in Paper 3 between demographic responses to shade and inter-annual drought. This trade-off promotes coexistence, because species specialise on coping with either shade or drought, increasing intraspecific competition under these conditions (Silvertown 2004).

In addition, host-specific natural enemies can have stabilizing effects on coexistence through density-dependent effects on plant communities (Chesson 2000). Originally proposed by Janzen (1970) and Connell (1971), the Janzen-Connell hypothesis states that host-specific pathogens or herbivores reduce survival of seeds or seedlings close to conspecific adults or in areas with high conspecific seedling density, particularly in wet ecosystems such as tropical forests (Comita et al. 2014). For many species in the BCI 50-ha plot, seedling densities shift away from adults over time (Murphy et al. 2017). Moreover, seedling survival of rare species on BCI is increased more by conspecific neighbours compared to common species, indicating that negative density dependence shapes species abundances (Comita et al. 2010). A study on taller seedlings ($\geq$ 20 cm tall and < 1 cm DBH) compared various factors influencing seedling survival on BCI and found that plant size was most important, followed by topographic habitats, negative density dependence and annual variation in water availability (Johnson et al. 2017). This is in line with my findings in Paper 2 that small seedlings are highly vulnerable and that spatial variation in water availability affects seedling mortality of taller seedlings indirectly by affecting their size. It also suggests that the effect of water availability and negative density dependence on seedling dynamics are of comparable strength on BCI.

Besides stabilising mechanisms, equalising mechanisms such as recruitment and dispersal limitation inhibit competitive exclusion in diverse species communities such as tropical forests (Hubbell 2009), particularly when stronger recruitment limitation of dominant species slows down competitive exclusion (Hurtt and Pacala 1995). There is strong dispersal and recruitment limitation on BCI, allowing inferior competitors to establish and coexist with better competitors (Hubbell et al. 1999, Harms et al. 2000). Dispersal limitation may confound observed habitat associations to

resources such as soil moisture, because species that have clumped distributions may be present in a certain habitat by chance (Plotkin et al. 2000). Patchy species distributions unrelated to environmental variation are common on BCI, which may be due to slow colonisation of parts of the island and the 50-ha plot by dispersal-limited species after the most recent human activity 100-200 years ago (Hubbell and Foster 1983, Svenning et al. 2004). I showed in Paper 2 that the distributions of fewer species were significantly associated to the soil moisture gradient when taking small-scale spatial aggregation into account, which was also the case for habitat associations of large trees (Harms et al. 2001). However, there were still significant associations for both life stages when taking spatial aggregation into account. These findings show that dispersal and recruitment limitation as well as niche differentiation along the soil moisture gradient contribute to species coexistence in tropical forests.

Finally, species diversity is affected by neutral processes such as ecological drift (Hubbell 2001). Ecological drift causes random fluctuations in species abundances and composition due to random birth and death (Vellend 2010). Species abundance distributions in the 50-ha plot on BCI can be explained by ecological drift in a neutral model (Chisholm and Pacala 2010). However, patterns that can be explained by neutral processes do not preclude the presence of niches (Chisholm and Pacala 2010) and the relative importance of niche and neutral processes for maintaining species diversity is an ongoing debate (e.g. Chase and Leibold 2003, Adler et al. 2007, Hérault 2007). In sum, my work indicates that niche differentiation of species along the soil moisture gradient and a trade-off in responses to shade and drought contribute to species coexistence on BCI and likely in other highly diverse tropical forests. Yet, these processes occur alongside other processes influencing species composition, abundances and diversity such as negative density dependence, recruitment and dispersal limitation and ecological drift (Svenning et al. 2004, Comita et al. 2014).

4.5 Outlook

In this section, I discuss how future work can build upon my findings to increase our knowledge about the role of soil moisture in tropical forests. In Paper 1, I used Random Forests to create maps of soil water potential based on predictors such as topography and soil type. The predictive performance of my model (R^2 = 0.41) may be improved with continuous information on soil properties that affect water availability for plants such as bulk density and pore size distribution

(Hodnett and Tomasella 2002, Juo and Franzluebbers 2003). However, continuous spatial data on these soil properties on BCI are currently not available. A recent study in the Brazilian Cerrado developed an approach for mapping soil variables such as bulk density on a local scale, combining relatively few soil samples with data on topography and soil type and expert knowledge (Menezes et al. 2018). This approach may be applied to the BCI 50-ha plot to improve the accuracy of soil water potential predictions with relatively little additional soil sampling effort.

In Paper 2 and 3, I studied how growth and mortality of species are affected by water and light availability. However, it remains unclear which traits cause the responses of species in my study to these resources. There is a wealth of functional trait data on species from BCI, ranging from morphological traits on roots, leaves and stems to physiological and hydraulic traits (see e.g. Kitajima 1994, Wright et al. 2010, Hietz et al. 2017). These data can be used to explore the drivers of the demographic responses of seedlings to light and water. For example, in Paper 3 I found a trade-off between responses to shade and drought, and acquisitive species had a stronger negative response drought in terms of survival than conservative species. High wood density is a trait that is responsible for both shade and drought tolerance (Wright et al. 2010, Poorter et al. 2019), so it would be interesting to see if conservative species in my study have a higher wood density. When the functional traits that are responsible for the demographic responses of the species in my studies are identified, information on these traits for other species can be used to better predict ecosystem functioning and diversity of tropical forests (Craine et al. 2012).

The relationship between the soil moisture niche and ecosystem functioning also remains unclear. Niche differences in underground resource use among species may increase complementary resource use, which would increase productivity and may make tropical forests better adapted to climate change (Schwinning and Kelly 2013, Turnbull et al. 2013). More generally, niche differences increase species diversity (see section 4.4), which enhances the resilience of ecosystems and ensures that they can provide valuable ecosystem services such as climate regulation (Hooper et al. 2005, Tilman et al. 2014). I quantified horizontal niche differentiation on a soil moisture gradient, while vertical niche differentiation with varying water uptake depths in tropical forests is also increasingly well understood (see section 4.2). Future work can use my soil moisture data in hydrological models to determine three-dimensional water

availability, in order to better understand the effect of soil moisture variation on various ecosystem functions and services such as water cycling and carbon sequestration.

Finally, my soil moisture maps (Paper 1) and estimates of species responses to shade and drought (Paper 2 and 3) can be combined with functional trait data to increase the accuracy of vegetation models, particularly to model the effect of climate change on tropical forests. Climate change is one of the major threats to tropical forests (Laurance and Peres 2006). Besides warming, rainfall patterns are expected to shift, leading to longer and more severe droughts (IPCC 2014). Combining empirical information (e.g. my species responses) with modelling approaches can improve our understanding of the effect of climate change on species composition and ecosystem functions such as carbon storage in tropical forests (van der Sande et al. 2017, Feng et al. 2018). Dynamic Global Vegetation Models (DGVMs) that include functional trait information showed that functional diversity can enhance the resilience in tropical forests to climate change in terms of biomass (Sakschewski et al. 2016). However, DGVMs cannot yet accurately capture increases in mortality rates due to climate change, which may yield unrealistic predictions of forest resilience (Galbraith et al. 2018). Thus, incorporating my species responses to drought (and potentially shade) in DGVMs may increase the accuracy of these models in predicting the effect of climate change on tropical forests. In addition, the code I provided in Paper 1 can be used to create custom maps of soil moisture on BCI for different dry season conditions. By varying dry season intensity, these maps can be used to more accurately predict the effect of climate change on local tropical tree species communities.

5. CONCLUSIONS

This dissertation deepens our understanding of the role of soil moisture in shaping tree species demography and distributions in the tropical moist forest on Barro Colorado Island (BCI), Panama. I measured a detailed gradient of soil water potential in the 50-ha plot on BCI. I used these data to create the first maps of soil water potential in a large permanent tropical forest plot. By providing small-scale spatial data of soil moisture, these maps improve upon the common approach of using soil type or topography to define habitats as a proxy for variation in soil moisture.

I quantified the importance of the soil moisture niche for the species community in terms of demographic responses of seedlings to soil moisture and compared the effects of soil moisture and light availability. I identified a novel mechanism shaping species distributions: species with a growth advantage in wetter sites were able to escape the vulnerable smaller size range, which decreases mortality and increases their abundance on the wet side of the soil moisture gradient. By promoting niche differentiation, soil moisture may contribute to the maintenance of species diversity in tropical forests. In addition, the distributions of seedlings along the soil moisture gradient were related to distributions in later life stages (saplings and trees). Yet, there were only few species with significantly different growth, mortality or distributions along the soil moisture gradient, indicating that small-scale soil water potential measurements are required to identify such mechanisms. Finally, I found a trade-off between demographic responses of species to inter-annual drought (i.e. intensity of the dry season) and shade, i.e. species are specialised in coping with either shade or drought. This trade-off may contribute to coexistence by preventing species to become dominant under all shade and drought conditions.

Niche differentiation on the soil moisture gradient and the trade-off between shade and drought responses are stabilising mechanisms that contribute to the maintenance of species diversity in the tropical moist forest on BCI. These mechanisms act in concert with other mechanisms that promote coexistence, such as negative density or distance dependence mortality. Future studies can use my soil water potential maps and my estimates of demographic responses to light and water availability to study the functional traits underlying the demographic responses to shade and drought, as well as the effects of shade and drought on the composition of local tropical tree species communities and ecosystem functioning of tropical forests under current and future climate conditions.

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LIST OF PUBLICATIONS

Kupers, S.J., Wirth C., Engelbrecht, B.M.J., Rüger, N. Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama. Scientific Data 6 (63):1–9 (2019). https://doi.org/10.1038/s41597-019-0072-z

Kupers, S.J., Engelbrecht, B.M.J., Hernández, A., Wright S.J., Wirth C., Rüger, N. Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings. Journal of Ecology **107**:860–874 (2019). https://doi.org/10.1111/1365-2745.13096

Gevaert A., **Kupers S.J.**, Heijman W., Participatory Landscape Planning: The case of the "Westvaardersplassen" in the Netherlands. Review of Agricultural and Applied Economics, 17(2): 92–102 (2014). https://doi.org/10.15414/raae.2014.17.02.92-102

PRESENTATIONS

Kupers S.J., Wirth C., Engelbrecht B.M.J., Hernández A., Wright S.J., Rüger, N. Shade and drought tolerance trade off in tropical seedlings: a demographic approach. (oral). Annual Meeting of the Association of Tropical Biology and Conservation (oral). Kuching, Malaysia, 2 July 2018.

Kupers S.J., Engelbrecht B.M.J., Wright S.J., Hernández A., Wirth C., Rüger, N. Demographic drivers of local species distributions: quantifying growth and mortality responses of tropical seedlings to soil moisture (oral). iDiv Annual Conference, Leipzig, Germany, 20 September 2017.

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PRESENTATIONS

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Kupers S.J., Engelbrecht B.M.J., Wright S.J., Wirth C., Rüger, N. The effect of soil moisture on seedling demography in Panama, European Conference of Tropical Ecology (oral). Göttingen, Germany, 24 February 2016.

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Paper 1

Dissertation

Stefan Kupers

The Soil Moisture Niche in a Moist Tropical Forest – A Demographic Approach

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Author contribution statement:

Title:	Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama
Journal:	Scientific Data
Authors:	Kupers, S.J., Wirth C., Engelbrecht, B.M.J., Rüger, N.

Stefan Kupers:
Designed research · Collected and processed data · Analysed data · Conceptualised the paper · Wrote the paper · Edited the paper · Submitted the paper

Christian Wirth:
Designed research · Contributed analytical tools · Edited the paper

Bettina Engelbrecht:
Edited the paper

Nadja Ruger:
Designed research · Conceptualised the paper · Edited the paper

Stefan Kupers

Christian Wirth

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Paper 2

Dissertation

Stefan Kupers

The Soil Moisture Niche in a Moist Tropical Forest – A Demographic Approach

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Author contribution statement:

Title: Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

Journal: Journal of Ecology

Authors: Kupers, S.J., Engelbrecht, B.M.J., Hernández, A., Wright S.J., Wirth C., Rüger, N.

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Paper 3

Author contribution statement:

Title:	Performance of tropical forest seedlings facing shade and drought: an interspecific trade-off in demographic responses
Journal:	Scientific Reports [in review]
Authors:	Kupers, S.J., Wirth, C., Engelbrecht, B.M.J., Hernández, A., Condit, R., Wright, S.J., Rüger, N.

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Christian Wirth

Nadja Rüger

DECLARATION OF INDEPENDENT WORK

I, Stefan Kupers, hereby affirm that I take note and accept the regulations for the doctorate degree at the Faculty of Life Sciences of the Leipzig University on 29th April 2015.

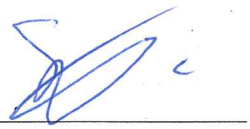
I further affirm that the presented dissertation was prepared autonomously without inadmissible help. All aids used in this dissertation and scientific ideas which were quoted from or based on other sources were cited at the respective point.

All people who helped me to prepare the conception, to select and analyse the materials of this dissertation as well as to improve the manuscript are namely cited in the acknowledgments. With exception of people mentioned by name, no other persons were involved in the intellectual work. No Ph.D. consultant service was employed. Third parties did not get money´s worth for benefits that were in conjunction with the content of this dissertation.

I declare that this dissertation has been neither presented nationally nor internationally in its entirety or in parts to any institution for the purpose of dissertation or other official or scientific examination and/or publishing.

Previously unsuccessful dissertations have not taken place.

Leipzig,
24.06.2019



Stefan Kupers

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SUPPLEMENTARY MATERIAL

Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

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SUPPORTING INFORMATION

This file includes:

Appendix S1 Supporting figures and tables

This appendix contains Figures S1.1-S1.8 and Tables S1.1-S1.3.

Figures S4-S6 are provided as separate pdf files. These figures show the responses of all species to soil water potential (SWP) and height in terms of growth > 0 (Fig. S4) and mortality rates (Fig. S5) as presented in the main text, as well as responses of growth ≤ 0 (Fig. S6) as presented in Appendix S3.

Tables S4-S7 are provided in an xlsx file. These tables contain observed and randomised species distributions along the SWP gradient (Table S4), the parameter estimates of the growth model (Table S5) and mortality model (Table S6) as presented in the main text, and parameter estimates of the model including growth ≤ 0 (Table S7).

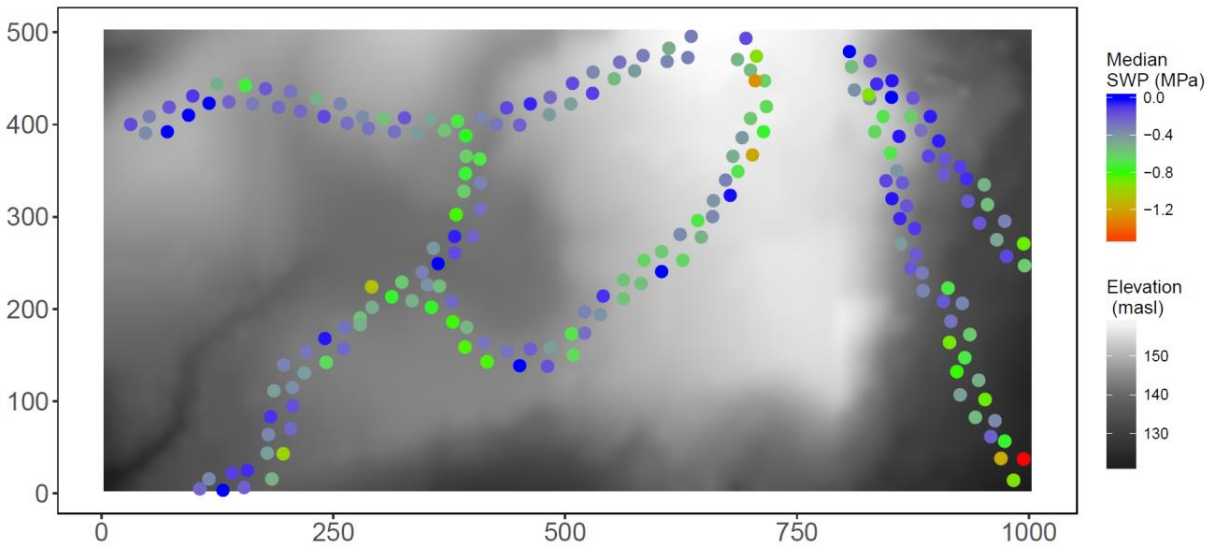

Figure S1.1 Soil water potential (SWP) at the 200 seedling census sites (coloured dots) in the 50-ha Forest Dynamics plot on Barro Colorado Island, Panama. Colours indicate the median SWP of the 2015 dry season (February, March, April) and the 2016 dry season (March).

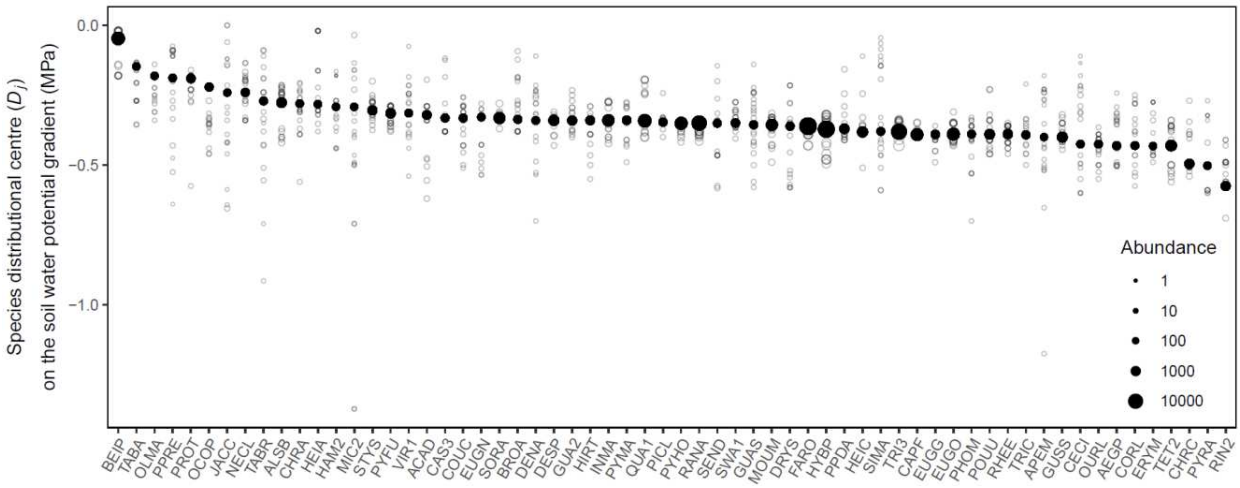

Figure S1.2 Distributional centres (D_j) of species on the soil water potential (SWP) gradient, quantified as the median SWP of all seedling observations across all years (black circles), and in each of the 20 census years (open circles). Table S4 provides a key to full species names for the 4-letter mnemonics along the horizontal axis.

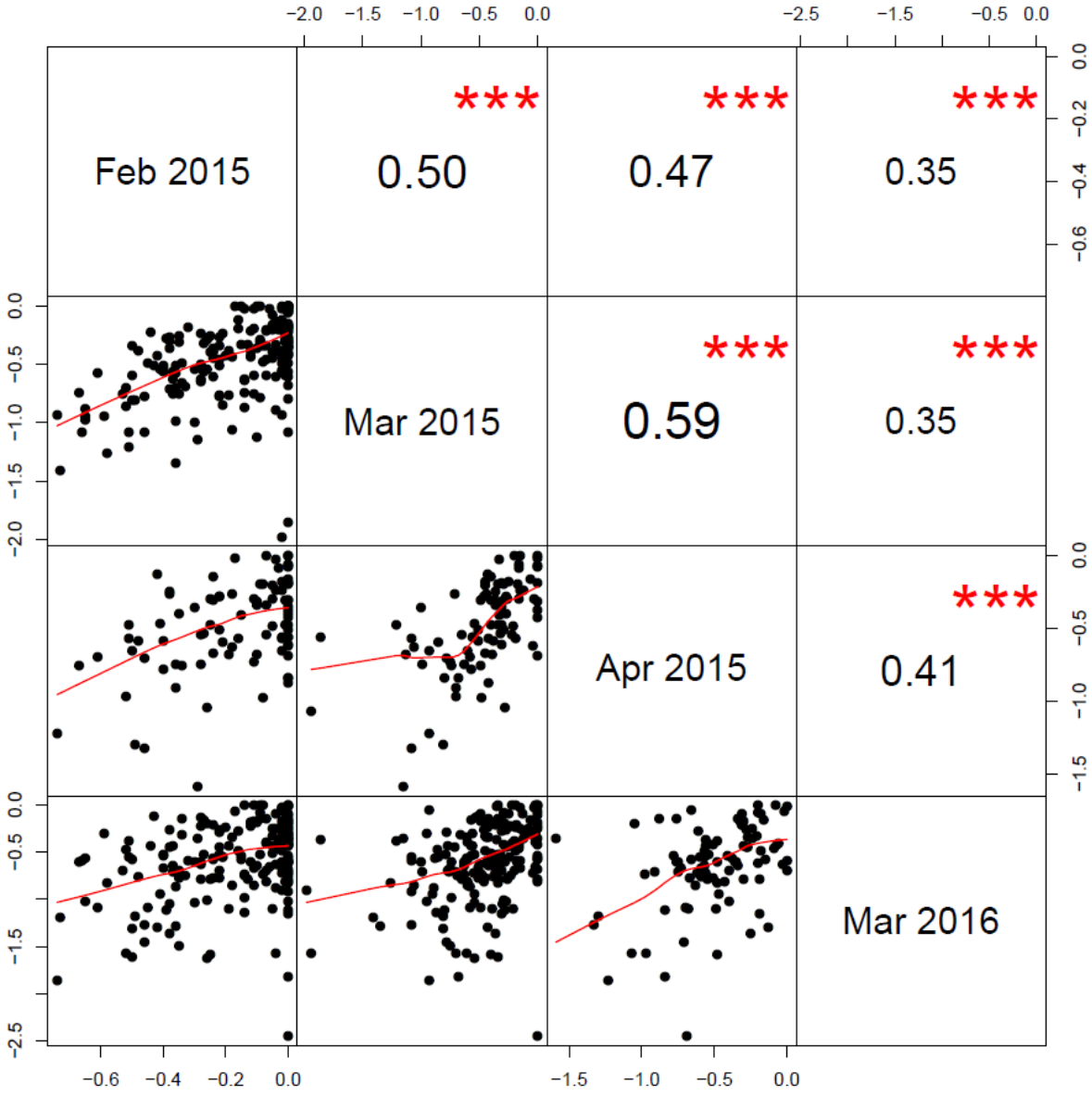

Figure S1.3 Pearson correlations of soil water potentials (MPa) measured at the sites among the four sampling periods. All correlations are significant at $p < 0.001$.

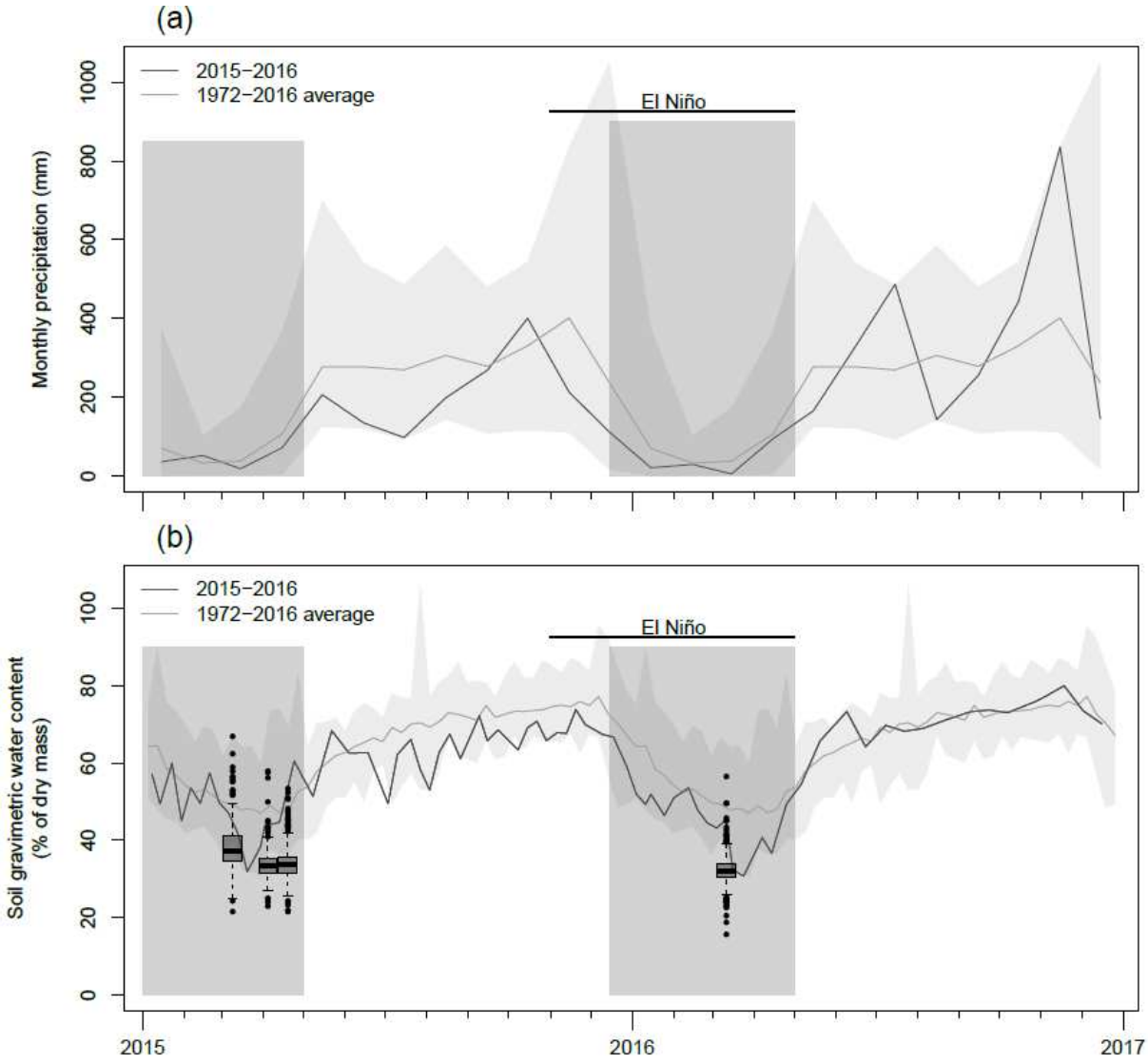

Figure S1.4 Monthly precipitation (a) and two-weekly gravimetric soil water content (b, SWC) on Barro Colorado Island (BCI), Panama. SWC (0-10 cm depth) is monitored in the Lutz catchment on BCI (1.25 km northeast of the 50-ha plot). Dark lines show values for the sampling period 2015 - 2016, and light lines show the long-term average. In (b), boxplots give the measured soil water content (SWC) we measured at 15 cm depth in the four sampling periods. Whiskers extend to ± 1.5 interquartile range. SWC in the 50-ha plot was lower than SWC at the monitoring site, likely because the sites differed in soil type (cf. Baillie, Elsenbeer, Barthold, Grimm, & Stallard 2007). Light grey shading indicates the range in precipitation and SWC of the long-term monitoring. Dry seasons run from mid-December to the end of April and are indicated with dark grey shading. The El Niño period is indicated with the horizontal black line, and is defined as having an Oceanic Niño Index ≥ 0.5 °C (NOAA, 2018). Precipitation and SWC monitoring data are from the Smithsonian Tropical Research Institute (STRI) Physical Monitoring Program (STRI, 2018).

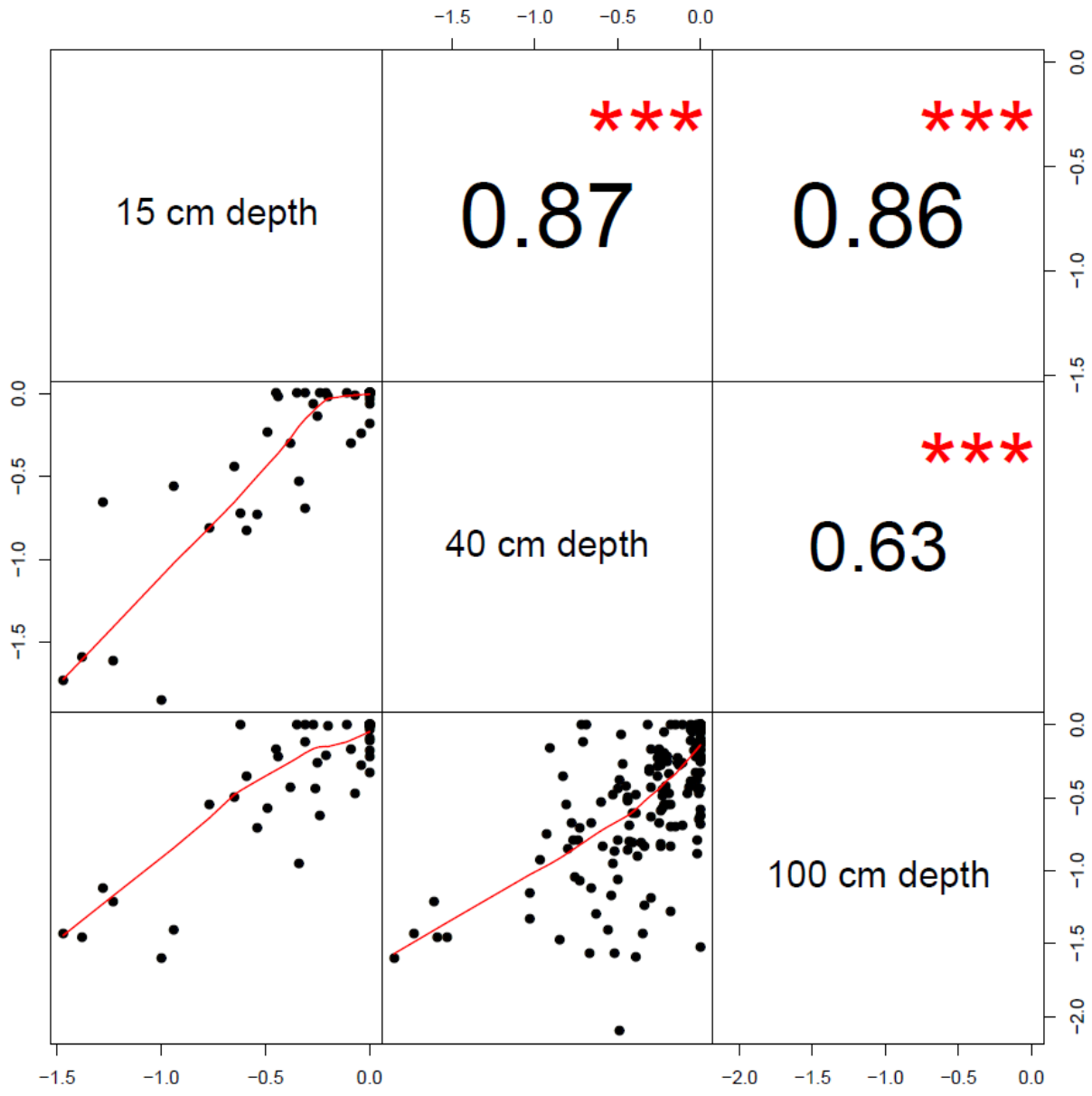

Figure S1.5 Pearson correlations of soil water potentials (MPa) at three depths. Samples were taken at a subset of the seedling sites (*n* = 36), as well as on the border of the 50-ha plot and in a 10-ha plot bordering the full northern side of the 50-ha plot (*n* = 66). All correlations are significant at *p* < 0.001.

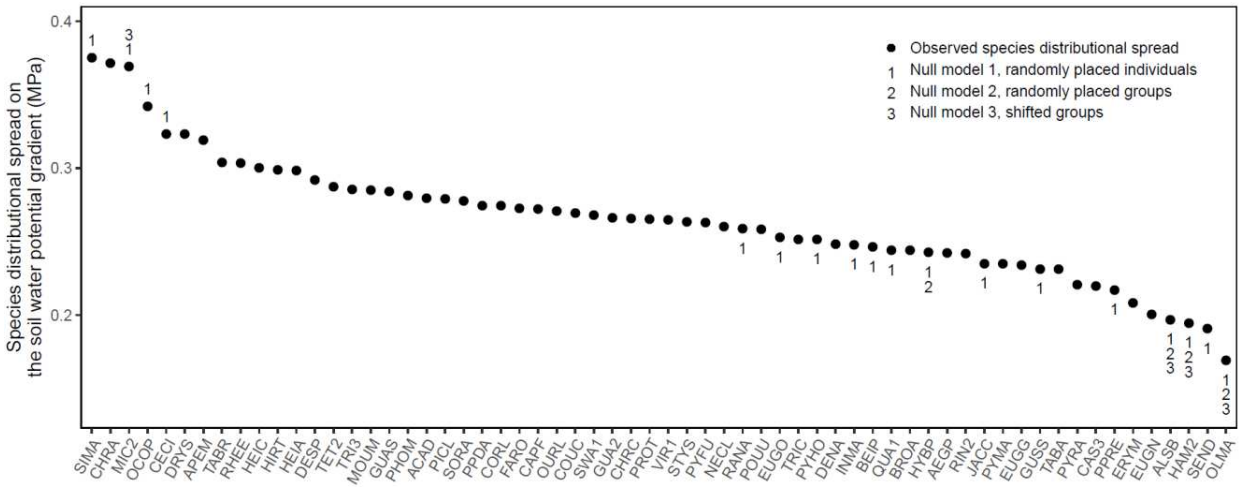

Figure S1.6 Distributional spread (D_j) of species on the local soil water potential (SWP) gradient. Species on the left side have a wider spread and species on the right side have a narrower spread. Distributional spread is the standard deviation SWP of the sites where the respective species occurs. Numbers indicate species for which distributional spreads are outside the 95% confidence interval of randomised values (see *Materials and Methods*). Shown are all 62 species with ≥ 100 positive growth and/or ≥ 100 mortality records. Table S4 provides a key to full species names for the 4-letter mnemonics along the horizontal axis.

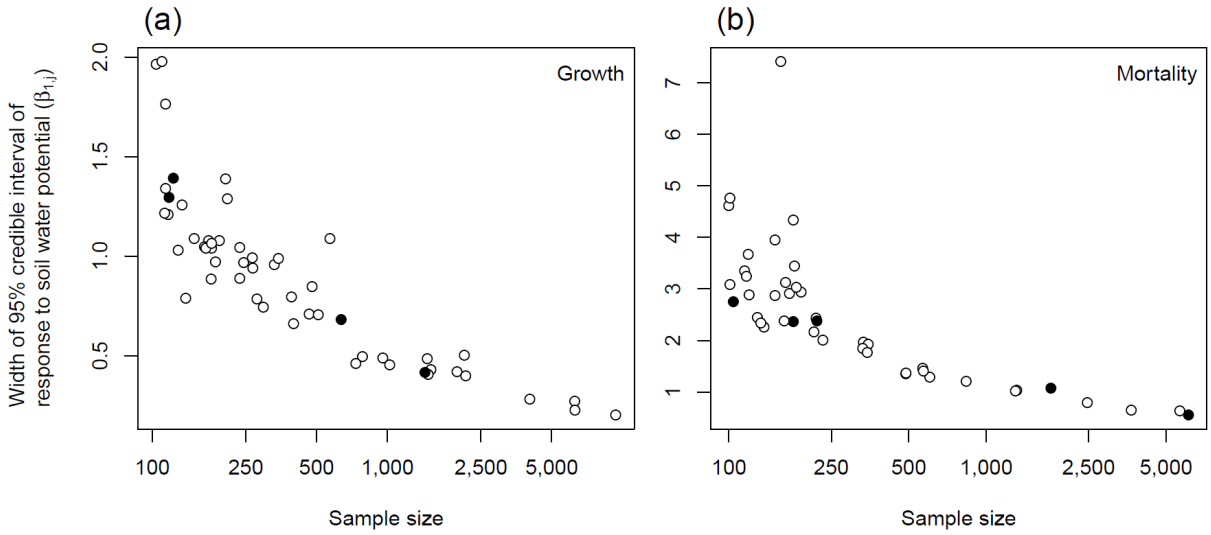

Figure S1.7 Width of the 95% credible interval of (a) growth and (b) mortality responses of species to soil water potential ($\beta_{1,j}$) presented in the main text versus sample size (i.e. the number of seedling observations of species in the respective models). Filled and unfilled circles represent species with significant and nonsignificant responses, respectively.

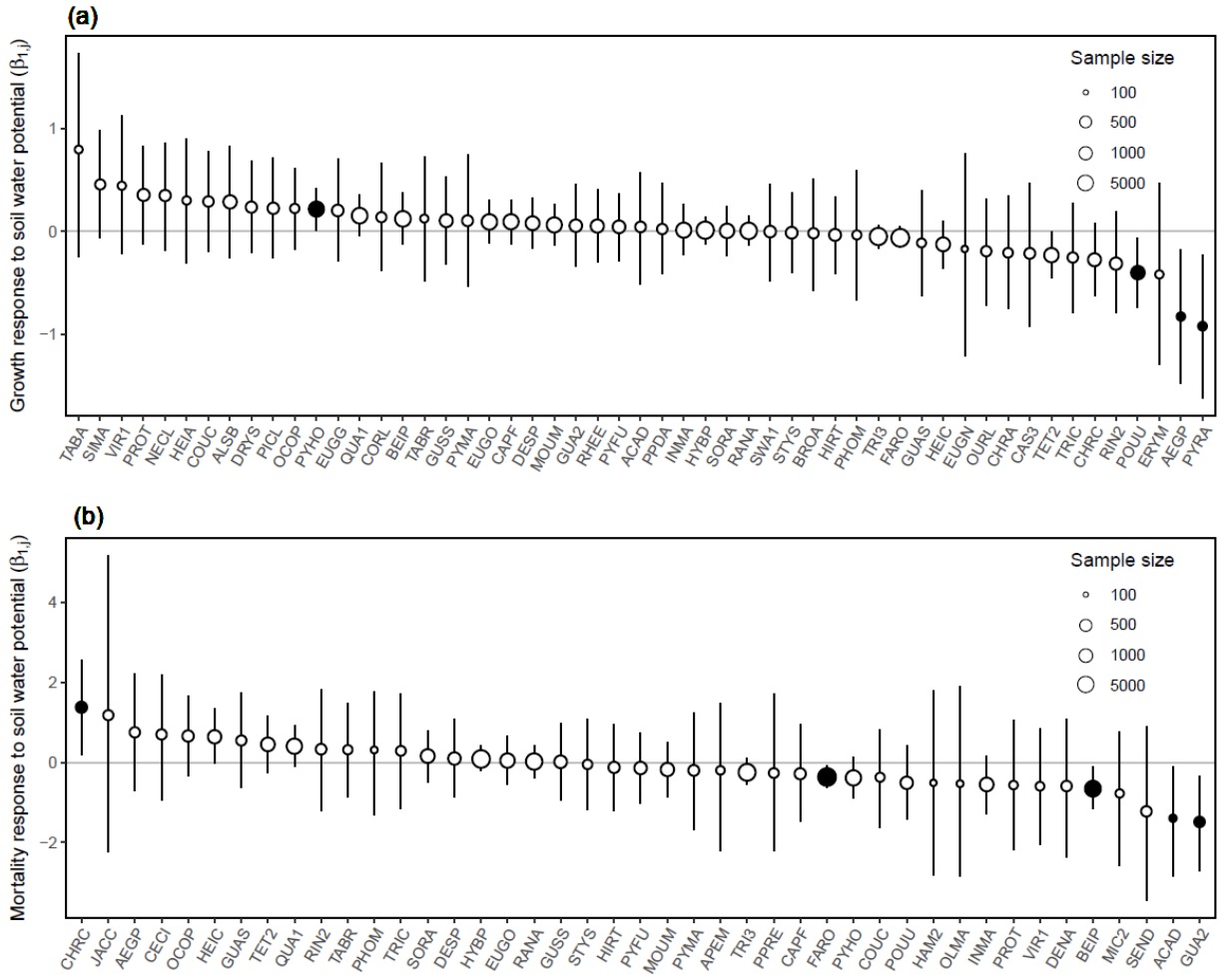

Figure S1.8 (a) Growth and (b) mortality responses to soil water potential (circles) and their 95% credible intervals (lines) of the models presented in the main text. Filled and unfilled circles represent species with significant and nonsignificant responses, respectively. Table S4 provides a key to full species names for the 4-letter mnemonics along the horizontal axis.

Table S1.1 Slopes (γ_1) of the species-level regression (main text equation 5) between distributional centres on the soil water potential (SWP) gradient (D_j) and growth and mortality responses to SWP ($\beta_{1,j}$) for the models presented in the main text and for additional models used to evaluate the robustness of the results.

Model	*n* obs.	*n* species	Slope of regression line (γ_1) 2.5%ile	5%ile	mean	95%ile	97.5%ile	R^2
Growth (excluding ≤ 0)								
Main model[a]	50,901	53	**0.0234**	**0.0381**	**0.1038**	**0.1698**	**0.1834**	0.2990
First year growth	11,128	19	-0.0232	**0.0192**	**0.1735**	**0.3338**	0.3644	0.2924
Including pathogens and herbivory	51,818	53	**0.0318**	**0.0447**	**0.1104**	**0.1754**	**0.1872**	0.2979
Mortality								
Main model[a]	31,246	43	-0.0755	-0.0667	-0.0232	0.0172	0.0239	0.1208
Incl. pathogens and herbivory	31,746	43	-0.0791	-0.0692	-0.0266	0.0127	0.0182	0.1220
Growth (including ≤ 0)								
Main model	60,516	53	-0.0337	**0.0212**	**0.2983**	**0.5662**	**0.6202**	0.2333
First year growth	12,621	19	-0.3699	-0.2200	0.4161	1.084	1.2414	0.2512
Including pathogens and herbivory	62,649	53	**0.0002**	**0.0472**	**0.3025**	**0.5570**	**0.6101**	0.2196

Bold and underlined parameter estimates of γ_1 are significant, i.e. the 95% credible interval (CI) did not include zero, and bold γ_1 parameters are significant on the 90% CI. The same species as in the models presented in the main text were included in all models, except for the first-year growth models.
R^2 for all models was calculated following Gelman and Hill (2007). [a]These models are presented in the main text.

Table S1.2 Slopes (γ_1) of the species-level regression (main text equation 5) between distributional centres on the SWP gradient (D_j) and demographic responses to SWP ($\beta_{1,j}$), using distributional centres of species calculated from the ten censuses with the most seedling observations. Species with ≥ 20 observations in the selected census were included in the models. Additionally, we performed a model using the median of the distributional centres of each single census (1994-2014).

Model	Year of distribution	*n obs* for distr.	*n* species	Slope of regression line (γ_1) 2.5%ile	5%ile	mean	95%ile	97.5%ile
Growth	2005	12,133	37	-0.0278	-0.0065	0.1572	0.3249	0.3578
main model	2006	11,425	35	-0.0117	**0.0175**	**0.1446**	**0.2839**	0.3126
(excl. ≤ 0)	2004	11,110	37	-0.0233	**0.0207**	**0.2139**	**0.4076**	0.4458
	2007	10,875	41	-0.0038	**0.0218**	**0.1540**	**0.2814**	0.3122
	1999	10,837	35	-0.0308	-0.0091	0.1176	0.2526	0.2823
	2001	10,666	37	**0.0607**	**0.09216**	**0.2086**	**0.3286**	**0.3478**
	2008	10,456	38	**0.0272**	**0.0548**	**0.1633**	**0.2839**	**0.3118**
	1998	10,227	36	-0.0532	-0.0213	0.1180	0.2489	0.2822
	2000	9,917	38	**0.0843**	**0.1056**	**0.2312**	**0.3525**	**0.3820**
	2009	9,504	37	**0.0750**	**0.0931**	**0.1916**	**0.2988**	**0.3152**
	median	200,362	53	**0.0122**	**0.0256**	**0.0884**	**0.1545**	**0.1699**
Mortality	2005	12,133	34	-0.1370	-0.1278	-0.0638	0.0081	0.0206
main model	2006	11,425	31	-0.1365	-0.1228	-0.0633	0.0005	0.0115
	2004	11,110	29	-0.1363	-0.1233	-0.0415	0.0327	0.0454
	2007	10,875	36	-0.0933	-0.0828	-0.0188	0.0445	0.0578
	1999	10,837	27	-0.1118	-0.1027	-0.0461	0.0118	0.0246
	2001	10,666	30	-0.1251	-0.1099	-0.0530	0.0023	0.0140
	2008	10,456	31	-0.0652	-0.0522	-0.0009	0.0505	0.0600
	1998	10,227	28	-0.1171	-0.1048	-0.0411	0.0371	0.0559
	2000[a]	9,917	31	-0.1487	**-0.1355**	**-0.0712**	**-0.0046**	0.0128
	2009	9,504	31	-0.0854	-0.0854	0.0045	0.0744	0.0744
	median	200,362	43	-0.0648	-0.0648	-0.0197	0.0187	0.0187

Bold and underlined parameter estimates of γ_1 are significant, i.e. the 95% credible interval (CI) did not include zero, and bold γ_1 parameters are significant on the 90% CI. [a]*Jacaranda copaia* was excluded, because its mortality response was a strong outlier ($\beta_{1,j}$ = 3.17), caused by its high overall mortality rate (see Fig. S5) that complicated fitting and by its clumped distributional centre in the selected census.

Table S1.3 Correlations between median soil water potential (SWP) measured at the seedling census sites and shade intensity, nutrient availability and soil chemistry. We calculated mean shade intensity at 0.5 m height per site from 12 annual plot-wide canopy censuses (data from Condit, 2018), in which the presence of absence of vegetation in six height layers was recorded (see Rüger, Huth, Hubbell, & Condit 2009, for details). Nutrient availability and soil chemistry were determined from soil samples at 10 cm depth across the plot (data from Wolf, Hubbell, Fricker, & Turner 2015). We determined nutrient and soil chemistry at the seedling sites using the measurement nearest to each site.

Variable	*p*	*r*
Al[a]	0.90	0.01
Al	0.75	-0.02
Base saturation	0.70	-0.03
C	**<0.01**	-0.21
Ca[a]	0.08	-0.12
Ca	0.12	-0.11
CN ratio	0.65	-0.03
Cu[a]	0.21	0.09
Effective cation exchange capacity	0.08	-0.13
Fe[a]	0.53	0.04
Fe	0.56	-0.04
K[a]	0.52	-0.05
K	0.95	0.00
Mg[a]	**0.01**	-0.17
Mg	**0.03**	-0.16
Mn[a]	0.98	0.00
Mn	0.62	0.04
N	**<0.001**	-0.25
Na	0.11	0.11
P[a]	0.11	-0.11
pH (salt)	0.42	-0.06
pH (water)	0.28	-0.08
Shade index	**<0.001**	0.27
Total exchangeable bases	0.10	-0.12
Zn[a]	0.31	-0.07

[a]Determined with Mehlich 3 soil extractants.

Appendix S2 Soil water retention curves to identify SWP outliers

To determine outliers in soil water potential (SWP) measurements, we constructed soil water retention curves for 25 seedling sites. These curves showed how SWP and soil water content (SWC) were related for a particular soil type, as the shape of the curves depends on textural and structural soil characteristics (Gupta & Larson, 1979). The sites were selected to cover all soil types (cf. Baillie et al., 2007) and topographic habitats (cf. Harms, Condit, Hubbell, & Foster 2001) of the 50-ha plot. As such, the curves represent different combinations of SWP and SWC that can be expected at the seedling sites, and substantial deviation of measurements from these curves likely indicates measurement error.

The retention curves were constructed using samples that were first used to measure SWP and SWC (see *Materials and Methods*). We added distilled water to the soil samples until saturation (0 MPa). Soils were then dried for approximately 30 minutes, weighted and measured for SWP. This procedure was repeated 6-13 time until SWP dropped below -7 MPa. We then fitted a third-order polynomial line to construct each curve, correcting positive SWP to 0 MPa.

To determine outliers in SWP, we calculated the standard deviation (SD) of the SWC (horizontally) and SWP (vertically) measured in all sampling rounds (excluding observations used for constructing the curves). Six SWP samples that deviated by more than 1 SD from the most extreme retention curves were outliers and were excluded from the analysis (Fig. S2.1).

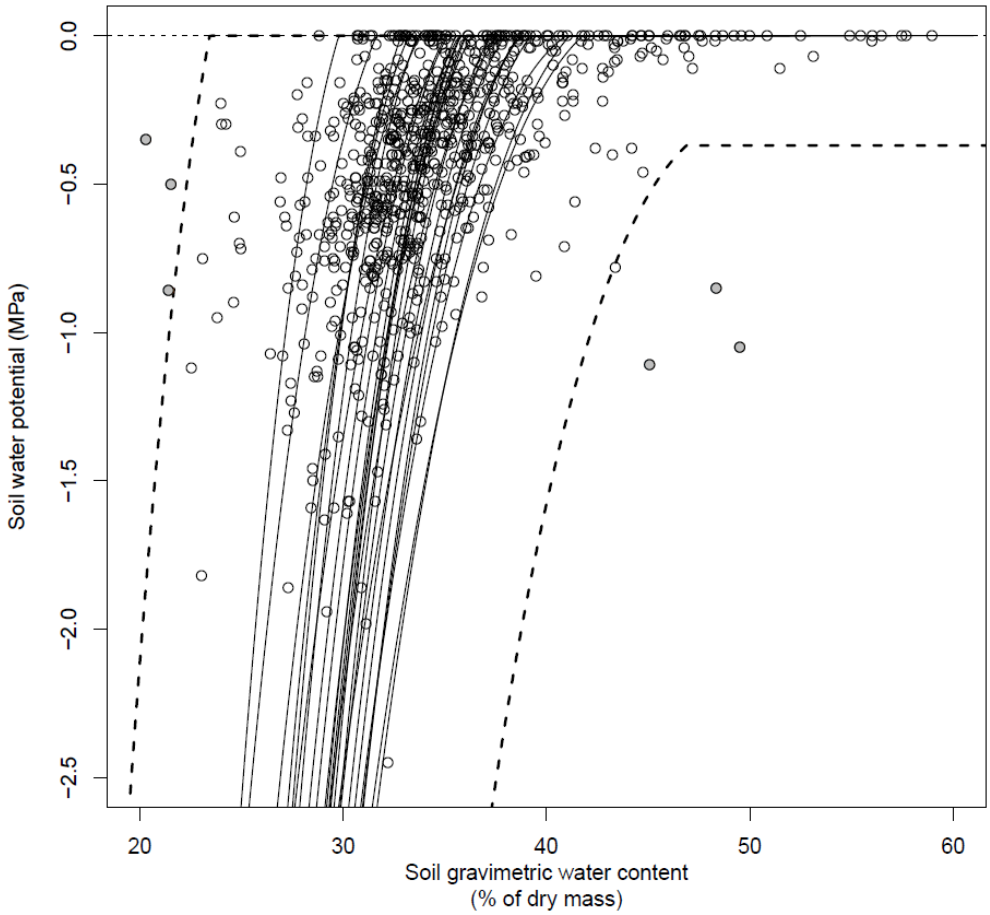

Figure S2.1 Soil water retention curves (solid lines) of 25 of the 200 seedling sites were used to identify outliers in observed soil water potential (dots). Outliers (grey dots) deviate more than 1 SD from the most extreme curves (dashed lines).

Appendix S3 Model including growth ≤ 0

We ran models including RGR (henceforth: growth) ≤ 0 to assess the potential bias from excluding growth ≤ 0. Whereas positive growth can be modelled using a lognormal distribution (see *Materials and Methods* in main text), this distribution cannot be used when negative growth values are included. One can include negative growth by using a normal distribution in the models, but this requires that the right skewed data is transformed using a power < 1 (Tukey, 1957). This works well for positive and negative growth through a modulus transformation (John & Draper, 1980):

$$RGR_t(\lambda) = \begin{cases} RGR^{\lambda} & RGR \geq 0 \\ -\{(-RGR)^{\lambda}\} & RGR < 0 \end{cases} \qquad (1)$$

where RGR_t is the transformed RGR. This transformation reduced skewness sufficiently for diameter growth rates of saplings and large trees when using λ between 0.3 and 0.6 (Condit, Pérez, Lao, Aguilar, & Hubbell 2017). We used λ = 0.6, as this most reduced the skewness in our data (i.e. the difference between median and mean growth was smallest). Additionally, we excluded outliers using a modified z-score (Iglewicz & Hoaglin, 1993). The same outliers we excluded here were also excluded from the models with only positive growth (presented in the main text). The model with growth ≤ 0 included 17,946 individuals (60,516 observations). We included the same 53 species as in the model with only positive growth, i.e. all species with ≥ 100 positive growth observations.

When we included negative growth rates, there were four species that had significantly slower growth at wetter sites (higher SWP), and one species that had significantly faster growth at wetter sites (Fig. S6, Table S7). The species-level relationship (γ_1) between distributional centres of species along the SWP gradient (D_j) and growth responses to SWP ($\beta_{1,j}$) was marginally significant (Fig. S3.1). There was no significant difference in fitted growth rates of dry or wet distributed species 'at home' (Table S3.1), but the wettest distributed 50% of species had a marginally significant 'home advantage' over the driest distributed 50% of species (Table S3.2). The slope (γ_1) was not significant in the model using only first-year growth but significant when pathogen and herbivory damage was included (Table S1.1).

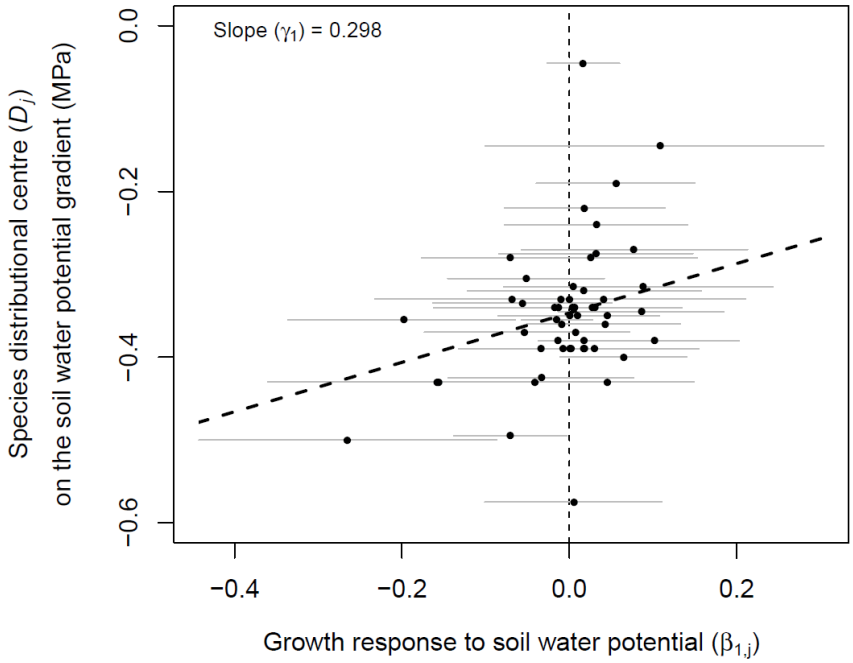

Figure S3.1 Relationship between distributional centres on the local soil water potential (SWP) gradient and growth responses of seedlings to SWP for the growth model including growth ≤ 0. Distributional centres on the SWP gradient are the median SWP of the sites where the species occurs (D_j, see *Materials and Methods*). The growth responses were fitted species-specific slopes for relationships between SWP and growth ($\beta_{1,j}$, see equation 3 in main text). Horizontal grey lines represent the 95% credible intervals (CI) of $\beta_{1,j}$. The relationship between distributional centres and SWP responses was the fitted slope of a linear regression fitted in the Bayesian model (γ_1, see equation 5 in main text), which is marginally significant on the 90% CI (dashed line, see Table S1.1).

Table S3.1 Test of the 'best at home' hypothesis for the model including growth ≤ 0 (Fig. S3.1). Shown are fitted growth rates of dry and wet distributed species at dry versus wet sites.

	Classification dry/wet species[a]	Dry sites[b] mean (SD)	Wet sites[b] mean (SD)	*t*	*df*	*p*
Growth (all values)						
Dry distributed	50%	0.300 (0.080)	0.284 (0.064)	0.742	27	0.464
species	33%	0.299 (0.090)	0.282 (0.071)	0.570	18	0.576
	25%	0.303 (0.094)	0.278 (0.065)	0.964	15	0.350
Wet distributed	50%	0.312 (0.064)	0.322 (0.067)	-1.571	24	0.129
species	33%	0.309 (0.070)	0.322 (0.075)	-1.200	16	0.247
	25%	0.304 (0.079)	0.323 (0.088)	-1.339	11	0.208

[a]Each analysis was repeated contrasting the 25%, 33% or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Fig. 1). [b]Dry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient, respectively.

Table S3.2 Test of the 'home advantage' hypothesis. Shown are fitted growth or mortality rates of dry versus wet distributed species at dry and wet sites. The bold and underlined value indicates significantly different mean performance ($p < 0.05$).

	Classification dry/wet species[a]	Dry distributed species mean (SD)	Wet distributed species mean (SD)	*t*	*df*	*p*
Growth (all values)						
Dry sites[b]	50%	0.300 (0.080)	0.312 (0.064)	-1.267	49.868	0.211
	33%	0.299 (0.090)	0.309 (0.070)	-1.034	32.590	0.309
	25%	0.303 (0.094)	0.304 (0.079)	-0.681	21.235	0.503
Wet sites[b]	50%	0.284 (0.064)	0.322 (0.067)	-2.068	47.173	**0.044**
	33%	0.282 (0.071)	0.322 (0.075)	-1.561	30.237	0.129
	25%	0.278 (0.065)	0.323 (0.088)	-1.367	17.177	0.189

[a]Each analysis was repeated contrasting the 25%, 33% or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Fig. 1). [b]Dry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient, respectively.

Appendix S4 Modelling details

4.1 Model implementation and diagnostics

We modelled posterior distributions, (hyper)parameters and error components using the Bayesian inference software package RStan version 2.16.2 (Stan Development Team, 2017) in R version 3.4.1 (R Core Team, 2017). We monitored convergence by running four chains with random starting values. We used the potential scale reduction factor (*Rhat*) to check for convergence of the model. *Rhat* did not exceed 1.1 for any of the parameters in any model, indicating that the models converged (Gelman & Hill, 2007). To prevent divergent transitions, we adapted the initial step size, target acceptance rate and maximum treedepth where necessary.

Chains of all models mixed well and converged in less than 100 iterations. For the models presented in the main text and the negative growth model excluding pathogens and herbivory (presented in Appendix S3), we used a burn-in period of 1,000 iterations and an additional 2,500 iterations after burn-in per chain, giving a total of 10,000 iterations for analyses (2,500 per chain). For all other models, we used 1,000 burn-in samples and 1,000 samples for analysis, giving a total of 2,000 samples for analyses (1,000 per chain). Correlations between parameters β_0, β_1 and β_2 were ≤ |0.40| for all models.

For each model, the proportion of explained variance (R^2) was calculated following Gelman and Hill (2007):

$$R^2 = 1 - \frac{\mathrm{E}\big(\mathrm{Var}(\epsilon)\big)}{\mathrm{E}\big(\mathrm{Var}(y)\big)} \qquad (2)$$

where ε are the residuals of all observations and samples after warmup and y are observed growth or mortality.

4.2 Test of phylogenetic signal

Phylogenetic relatedness might partly explain how species distributions along the SWP gradient relate to demographic responses to SWP. We tested for phylogenetic signal in the residuals of the species-level relationship between growth or mortality responses to SWP ($\beta_{1,j}$) and species distributional centres (D_j) (Revell, 2010). We estimated the phylogenetic signal in terms of Blomberg's K (Blomberg, Garland Jr, & Ives 2003) and Pagel's λ (Pagel, 1999). We used a phylogeny from Phylomatic (Webb, Ackerly, & Kembel 2008) and provided by Pearse, Jones, and Purvis (2013), which contained all species on BCI. There was no phylogenetic signal in any of the models, except for the first-year growth models in terms of Pagel's λ (Table S4.1). Therefore, we did not to correct for phylogenetic signal in the relationship between distributional centres of species and demographic responses.

Table S4.1 Phylogenetic signal in the residuals of the relationship between growth or mortality responses to SWP ($\beta_{1,j}$) and distributional centres of species (D_j). Bold and underlined values indicate significant phylogenetic signal ($p < 0.05$).

	Blomberg's K		Pagel's λ	
	K	*p*	λ	*p*
Growth (excluding ≤ 0)				
Main model	0.531	0.332	0.164	0.424
First year growth	1.279	0.102	1.000	**0.041**
Incl. pathogens and herbivory	0.537	0.317	0.178	0.374
Mortality				
Main model	0.582	0.254	0.184	0.548
Incl. pathogens and herbivory	0.571	0.305	0.068	0.964
Growth (including ≤ 0)				
Main model	0.550	0.257	0.171	0.401
First year growth	1.458	**0.066**	1.000	**0.016**
Incl. pathogens and herbivory	0.561	0.229	0.210	0.286

4.3 Stan code

4.3.1 Growth

```
data {
  int<lower=0>                                  N_obs;
  int<lower=0>                                  N_ind;
  int<lower=0>                                  N_year;
  int<lower=0>                                  N_sp;
  int<lower=0>                                  N_trap;

  real                                          obs[N_obs];

// we centred swp and height on 10 cm and -0.4 MPa, respectively, to weaken the correlation of the
// intercept (beta0) with the swp and height responses (beta1 and beta2, respectively) and to
// speed up convergence.
  vector[N_obs]                                 swp;
  vector[N_obs]                                 height;

  vector[N_sp]                                  d;

  int<lower=0>                                  species[N_obs];
  int<lower=0>                                  spind[N_ind];
  int<lower=0>                                  ind[N_obs];
  int<lower=0>                                  year[N_obs];
  int<lower=0>                                  trap[N_obs];

// repind indicates if an individual has multiple observations. We used this to determine if a random
// individual effect was needed for an individual.
  int<lower=0>                                  repind[N_ind];
}

parameters {
  real<lower=-10,upper=10>                      beta0[N_sp];
  real<lower=-10,upper=10>                      beta1[N_sp];
  real<lower=-10,upper=10>                      beta2N_sp];

  vector<lower=-10,upper=10>[N_year]            u_year;
  vector<lower=-10,upper=10>[N_ind]             u_ind;
  vector<lower=-10,upper=10>[N_trap]            u_trap;

//hyperparameters
  real<lower=-10,upper=10>                      mu_beta0;
  real<lower=-10,upper=10>                      mu_beta2;
  real<lower=-10,upper=10>                      gamma0;
  real<lower=-10,upper=10>                      gamma1;

  real<lower=-10,upper=10>                      mu_sigp;
  real<lower=-10,upper=10>                      mu_siguind;

  real<lower=0,upper=2>                         sigma_beta0;
  real<lower=0,upper=2>                         sigma_ beta2;
  real<lower=0,upper=2>                         sigma_d;
```

```
  vector<lower=0,upper=2>[N_sp]                    sigma_p;
  vector<lower=0,upper=2>[N_sp]                    sigma_uind;

  real<lower=0,upper=2>                            sigma_year;
  real <lower=0>                                   sigma_trap;
  real<lower=0,upper=2>                            sigma_sigp;
  real<lower=0,upper=2>                            sigma_siguind;
}

model{
  real pred[N_obs];
  beta0 ~ normal(mu_beta0,sigma_beta0);
  beta2 ~ normal(mu_beta2,sigma_beta2);

  for(i in 1:N_sp){
          d[i] ~ normal(gamma0 + gamma1 * beta1[i], sigma_d);
          }

  for(i in 1:N_trap){
          u_trap[i] ~ normal(0,sigma_trap);
          }

  u_year ~ normal(0,sigma_year);

  for( i in 1:N_ind){
          if(repind[i] == 1){
                  u_ind[i] ~ normal(0,sigma_uind[spind[i]]);
                  }
          }

// We changed all lognormal() distributions below to normal() in models including negative growth (See
// Appendix S3 for details).
  sigma_uind ~ lognormal(mu_siguind, sigma_siguind);
  sigma_p ~ lognormal(mu_sigp,sigma_sigp);
  for( i in 1:N_obs ){
    if( repind[ind[i]] == 1 ){
          pred[i] = u_ind[ind[i]] + u_trap[trap[i]] + u_year[year[i]] + beta0[species[i]] + beta1[species[i]] *
          swp[i] + beta2[species[i]] * log(height[i]);
                  }
                  else{
          pred[i] =                  u_trap[trap[i]] + u_year[year[i]] + beta0[species[i]] + beta1[species[i]] *
          swp[i] + beta2[species[i]] * log(height[i]);
          }
    obs[i] ~ lognormal ( pred[i], sigma_p[species[i]] );
  }
}
```

4.3.2 Mortality

```
data {
  int<lower=0>                                  N_ind;
  int<lower=0>                                  N_year;
  int<lower=0>                                  N_sp;
  int<lower=0>                                  N_trap;

  int<lower=0,upper=1>                          alive[N_ind];

// we centred swp and height on 10 cm and -0.4 MPa, respectively, to weaken the correlation of the
// intercept (beta0) with the swp and height responses (beta1 and beta2, respectively) and to
// speed up convergence.
  vector[N_ind]                                 swp;
  vector[N_ind]                                 height;

  vector[N_sp]                                  d;

  int<lower=0>
  int<lower=0>
  int<lower=0>                                  trap[N_ind];
}

parameters {
  real<lower=-10,upper=10>                      beta0[N_sp];
  real<lower=-10,upper=10>                      beta1[N_sp];
  real<lower=-10,upper=10>                      beta2[N_sp];

  real<lower=-10,upper=10>                      u_year[N_year];
  real<lower=-10,upper=10>                      u_trap[N_trap];

//hyperparameters
  real<lower=-10,upper=10>                      mu_beta0;
  real<lower=-10,upper=10>                      mu_beta2;
  real<lower=-10,upper=10>                      gamma0;
  real<lower=-10,upper=10>                      gamma1;

  real<lower=0,upper=2>                         sigma_year;
  real <lower=0>                                sigma_trap;
  real<lower=0,upper=2>                         sigma_beta0;
  real<lower=0,upper=2>                         sigma_beta2;
  real<lower=0,upper=2>                         sigma_d;
}
transformed parameters {
  vector[N_ind]                                 theta;
  real m;

  real mlog;

  for (i in 1:N_ind){
          m = u_trap[trap[i]] + u_year[year[i]] + beta0[species[i]] + beta1[species[i]] * swp[i] +
          beta2[species[i]] * log(height[i]);
          mlog = 1/(1+exp(-m));
          theta[i] = 1-mlog;
          }
}
```

```
model {
  beta0 ~ normal (mu_beta0, sigma_beta0);
  beta2 ~ normal (mu_beta2, sigma_beta2);

  for(i in 1:N_sp){
          d[i] ~ normal(gamma0 + gamma1 * beta1[i], sigma_d);
          }

  for(i in 1:N_trap){
          u_trap[i] ~ normal(0,sigma_trap);
          }

  for(i in 1:N_year){
          u_year[i] ~ normal(0,sigma_year);
          }

  for (i in 1:N_ind){
          alive[i] ~ bernoulli(theta[i]);
          }
}
```

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Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

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This file includes:

Table S4, containing observed and randomised distributional centres and spread of species along the soil water potential (SWP) gradient for all species in the study.

Table S5, containing parameter estimates of the growth model including only growth > 0 (presented in the main text).

Table S6, containing parameter estimates of the mortality model (presented in the main text).

Table S7, containing parameter estimates of the growth model additionally including growth ≤ 0 (presented in Appendix S3).

Table S4 Distributional centres (median) and spread (SD) of species on the soil water potential (SWP) gradient for all 62 species included in the study. Observed distributional centres of species were calculated for all seedling observations across all censuses collectively (see Fig. S1.2 for individual censuses). CI- and CI+ indicate the 2.5th and 97.5th percentiles, respectively, of randomised values of distributions generated with three increasingly conservative null models (see *Materials and Methods*). Bold and underlined CIs indicate null models for which the observed distributional centre of the species differed significantly from random distributions. Species among the 25%, 33% or 50% of the driest or wettest distributional centres were used to test the 'best at home' and 'home advantage' hypotheses. The 4-letter mnemonics (i.e. species codes) are used to indicate species in Fig. 1 and Figs. S1.2, S1.6 and S1.8.

		Sample	Classification of			Distributional centre on SWP gradient							Distributional spread on SWP gradient						
	Species	size	distribution				Null-model 1		Null-model 2		Null-model 3			Null-model 1		Null-model 2		Null-model 3	
Species	code	(*n*)	25%	33%	50%	Obs	CI-	CI+	CI-	CI+	CI-	CI+	Obs	CI-	CI+	CI-	CI+	CI-	CI+
Acalypha diversifolia	ACAD	620		wet	wet	-0.320	-0.440	-0.280	-0.510	-0.248	-0.500	-0.247	0.280	0.226	0.336	0.192	0.377	0.200	0.372
Aegiphila panamensis	AEGP	389	dry	dry	dry	-0.430	-0.430	-0.290	-0.465	-0.280	-0.490	-0.270	0.242	0.230	0.340	0.218	0.349	0.213	0.368
Alseis blackiana	ALSB	1147	wet	wet	wet	-0.275	**-0.430**	**-0.290**	-0.505	-0.245	-0.550	-0.250	0.197	**0.225**	**0.335**	**0.202**	**0.365**	**0.201**	**0.369**
Apeiba membranacea	APEM	169	dry	dry	dry	-0.400	-0.430	-0.295	-0.460	-0.280	-0.480	-0.275	0.319	0.233	0.326	0.219	0.348	0.213	0.350
Beilschmiedia pendula	BEIP	5076	wet	wet	wet	-0.045	**-0.373**	**-0.340**	**-0.575**	**-0.180**	**-0.630**	**-0.179**	0.246	**0.262**	**0.290**	0.166	0.412	0.160	0.410
Brosimum alicastrum	BROA	390			wet	-0.335	-0.478	-0.270	-0.520	-0.215	-0.555	-0.200	0.244	0.216	0.354	0.193	0.381	0.189	0.373
Capparis frondosa	CAPF	3407	dry	dry	dry	-0.390	-0.400	-0.330	-0.430	-0.295	-0.430	-0.290	0.272	0.246	0.309	0.232	0.325	0.231	0.326
Cassipourea elliptica	CAS3	372		wet	wet	-0.330	-0.500	-0.270	-0.600	-0.180	-0.621	-0.185	0.219	0.210	0.374	0.171	0.424	0.165	0.386
Cecropia insignis	CECI	260	dry	dry	dry	-0.425	**-0.410**	**-0.318**	-0.490	-0.270	-0.485	-0.270	0.323	**0.240**	**0.314**	0.209	0.359	0.212	0.352
Chrysophyllum argenteum	CHRA	261	wet	wet	wet	-0.280	-0.530	-0.245	-0.535	-0.220	-0.550	-0.195	0.371	0.194	0.375	0.190	0.394	0.184	0.392
Chrysophyllum cainito	CHRC	877	dry	dry	dry	-0.495	**-0.415**	**-0.315**	**-0.490**	**-0.275**	-0.495	-0.270	0.265	0.236	0.317	0.217	0.354	0.211	0.369
Cinnamomum triplinerve	PHOM	318	dry	dry	dry	-0.390	-0.460	-0.277	-0.490	-0.270	-0.500	-0.239	0.281	0.221	0.341	0.204	0.369	0.206	0.367
Cordia lasiocalyx	CORL	334	dry	dry	dry	-0.430	-0.465	-0.272	-0.510	-0.240	-0.510	-0.240	0.274	0.214	0.354	0.204	0.380	0.204	0.383
Coussarea curvigemmia	COUC	384		wet	wet	-0.330	-0.430	-0.280	-0.500	-0.245	-0.530	-0.220	0.269	0.226	0.336	0.205	0.375	0.195	0.362
Dendropanax arboreus	DENA	277			wet	-0.340	-0.415	-0.315	-0.430	-0.295	-0.431	-0.280	0.248	0.240	0.315	0.231	0.329	0.235	0.325
Desmopsis panamensis	DESP	1551			wet	-0.340	-0.415	-0.320	-0.440	-0.280	-0.480	-0.270	0.292	0.245	0.314	0.227	0.330	0.222	0.341
Drypetes standleyi	DRYS	424			dry	-0.360	-0.480	-0.270	-0.510	-0.245	-0.520	-0.215	0.323	0.210	0.348	0.199	0.372	0.169	0.405
Erythroxylum macrophyllum	ERYM	201	dry	dry	dry	-0.430	-0.535	-0.220	-0.535	-0.215	-0.520	-0.200	0.208	0.187	0.393	0.183	0.385	0.180	0.414
Eugenia galalonensis	EUGG	494	dry	dry	dry	-0.390	-0.460	-0.275	-0.530	-0.230	-0.535	-0.205	0.234	0.212	0.342	0.189	0.382	0.198	0.384
Eugenia nesiotica	EUGN	265		wet	wet	-0.330	-0.555	-0.200	-0.560	-0.195	-0.555	-0.220	0.200	0.176	0.390	0.176	0.414	0.171	0.403
Eugenia oerstediana	EUGO	3867	dry	dry	dry	-0.390	-0.390	-0.335	-0.430	-0.305	-0.430	-0.305	0.253	**0.254**	**0.299**	0.238	0.326	0.238	0.324

Faramea occidentalis	FARO	21617			dry	-0.360	-0.360	-0.345	-0.395	-0.335	-0.395	-0.330	0.273	0.268	0.284	0.252	0.302	0.253	0.303
Garcinia intermedia	RHEE	910	dry	dry	dry	-0.390	-0.430	-0.280	-0.460	-0.277	-0.460	-0.275	0.303	0.222	0.339	0.212	0.347	0.215	0.350
Guapira standleyana	GUAS	386			dry	-0.355	-0.430	-0.280	-0.490	-0.270	-0.463	-0.270	0.284	0.228	0.335	0.215	0.361	0.219	0.349
Guarea guidonia	GUA2	747			wet	-0.340	-0.430	-0.295	-0.440	-0.290	-0.495	-0.275	0.266	0.234	0.321	0.228	0.334	0.216	0.347
Gustavia superba	GUSS	1384	dry	dry	dry	-0.400	-0.400	-0.320	-0.480	-0.275	-0.466	-0.247	0.231	**0.246**	**0.308**	0.215	0.349	0.214	0.339
Hampea appendiculata	HAM2	195	wet	wet	wet	-0.290	-0.440	-0.290	-0.490	-0.270	-0.500	-0.250	0.194	**0.225**	**0.334**	**0.213**	**0.361**	**0.211**	**0.354**
Heisteria acuminata	HEIA	235	wet	wet	wet	-0.280	-0.520	-0.240	-0.745	-0.060	-0.740	-0.060	0.298	0.196	0.375	0.146	0.403	0.153	0.426
Heisteria concinna	HEIC	1605		dry	dry	-0.380	-0.400	-0.320	-0.495	-0.270	-0.510	-0.270	0.300	0.248	0.308	0.214	0.359	0.214	0.364
Hirtella triandra	HIRT	648			wet	-0.340	-0.430	-0.305	-0.430	-0.290	-0.490	-0.280	0.298	0.235	0.326	0.221	0.338	0.221	0.340
Hybanthus prunifolius	HYBP	17041			dry	-0.370	**-0.360**	**-0.345**	-0.410	-0.315	-0.420	-0.315	0.242	**0.267**	**0.286**	**0.245**	**0.317**	0.238	0.315
Inga marginata	INMA	2889			wet	-0.340	-0.390	-0.335	-0.430	-0.305	-0.441	-0.290	0.248	**0.253**	**0.300**	0.236	0.331	0.227	0.341
Jacaranda copaia	JACC	189	wet	wet	wet	-0.240	**-0.425**	**-0.310**	-0.550	-0.205	-0.560	-0.240	0.235	**0.236**	**0.318**	0.193	0.390	0.183	0.388
Miconia argentea	MIC2	200	wet	wet	wet	-0.290	-0.430	-0.290	-0.520	-0.240	-0.511	-0.220	0.369	**0.231**	**0.327**	0.198	0.391	**0.199**	**0.364**
Mouriri myrtilloides	MOUM	2637			dry	-0.355	-0.400	-0.330	-0.460	-0.280	-0.480	-0.280	0.285	0.248	0.307	0.228	0.340	0.225	0.343
Nectandra lineata	NECL	427	wet	wet	wet	-0.240	**-0.430**	**-0.280**	-0.520	-0.240	-0.560	-0.229	0.260	0.219	0.346	0.200	0.369	0.187	0.367
Ocotea puberula	OCOP	418	wet	wet	wet	-0.220	**-0.430**	**-0.300**	-0.540	-0.215	-0.536	-0.195	0.342	**0.237**	**0.328**	0.205	0.386	0.204	0.374
Ouratea lucens	OURL	302	dry	dry	dry	-0.425	-0.525	-0.240	-0.555	-0.200	-0.590	-0.190	0.271	0.190	0.381	0.178	0.400	0.171	0.377
Picramnia latifolia	PICL	426			wet	-0.345	-0.493	-0.270	-0.540	-0.240	-0.510	-0.240	0.279	0.213	0.364	0.191	0.371	0.196	0.370
Piper darienense	PPDA	917			dry	-0.370	-0.440	-0.280	-0.540	-0.200	-0.575	-0.215	0.274	0.226	0.331	0.182	0.379	0.180	0.384
Piper reticulatum	PPRE	262	wet	wet	wet	-0.190	**-0.420**	**-0.312**	-0.600	-0.180	-0.630	-0.150	0.217	**0.237**	**0.321**	0.190	0.370	0.186	0.381
Pouteria reticulata	POUU	1205	dry	dry	dry	-0.390	-0.410	-0.320	-0.490	-0.270	-0.490	-0.250	0.258	0.244	0.310	0.221	0.354	0.217	0.361
Protium tenuifolium	PROT	568	wet	wet	wet	-0.190	**-0.440**	**-0.275**	**-0.520**	**-0.240**	**-0.535**	**-0.200**	0.265	0.220	0.336	0.203	0.365	0.182	0.388
Psychotria hoffmannseggiana	PYFU	986	wet	wet	wet	-0.315	**-0.405**	**-0.320**	-0.430	-0.280	-0.480	-0.275	0.263	0.245	0.313	0.229	0.337	0.224	0.337
Psychotria horizontalis	PYHO	4008			dry	-0.350	-0.380	-0.340	-0.430	-0.295	-0.431	-0.295	0.251	**0.261**	**0.294**	0.236	0.329	0.234	0.325
Psychotria marginata	PYMA	532			wet	-0.340	-0.440	-0.280	-0.500	-0.250	-0.505	-0.270	0.235	0.228	0.339	0.207	0.367	0.205	0.368
Psychotria racemosa	PYRA	229	dry	dry	dry	-0.500	**-0.490**	**-0.270**	-0.575	-0.190	-0.600	-0.185	0.221	0.205	0.352	0.174	0.404	0.164	0.389
Quararibea asterolepis	QUA1	4925			wet	-0.340	-0.375	-0.340	-0.480	-0.270	-0.520	-0.270	0.244	**0.260**	**0.294**	0.223	0.355	0.217	0.364
Randia armata	RANA	9758			dry	-0.350	-0.370	-0.340	-0.430	-0.290	-0.430	-0.290	0.258	**0.264**	**0.292**	0.239	0.328	0.229	0.334
Rinorea sylvatica	RIN2	843	dry	dry	dry	-0.575	**-0.430**	**-0.290**	**-0.550**	**-0.200**	-0.575	-0.195	0.242	0.231	0.324	0.176	0.388	0.174	0.374
Senna dariensis	SEND	317			dry	-0.350	-0.420	-0.305	-0.555	-0.200	-0.561	-0.185	0.191	**0.239**	**0.328**	0.182	0.384	0.186	0.382
Simarouba amara	SIMA	318		dry	dry	-0.380	-0.460	-0.275	-0.550	-0.215	-0.565	-0.215	0.375	**0.219**	**0.348**	0.186	0.391	0.178	0.384
Sorocea affinis	SORA	2312		wet	wet	-0.330	-0.395	-0.330	-0.430	-0.290	-0.430	-0.295	0.278	0.251	0.305	0.234	0.323	0.231	0.330

Stylogyne turbacensis	STYS	756	wet	wet	wet	-0.305	-0.430	-0.290	-0.495	-0.270	-0.520	-0.250	0.263	0.229	0.330	0.208	0.349	0.207	0.359
Swartzia simplex_var.grandiflora	SWA1	560			dry	-0.350	-0.495	-0.270	-0.500	-0.270	-0.495	-0.270	0.268	0.204	0.354	0.198	0.371	0.193	0.380
Tabebuia rosea	TABR	328	wet	wet	wet	-0.270	**-0.430**	**-0.280**	-0.510	-0.230	-0.535	-0.240	0.304	0.227	0.329	0.200	0.372	0.193	0.381
Tabernaemontana arborea	TABA	213	wet	wet	wet	-0.145	**-0.510**	**-0.240**	**-0.535**	**-0.230**	**-0.535**	**-0.230**	0.231	0.197	0.382	0.194	0.383	0.191	0.374
Tetragastris panamensis	TET2	1943	dry	dry	dry	-0.430	**-0.400**	**-0.330**	-0.500	-0.248	-0.510	-0.240	0.287	0.250	0.306	0.211	0.360	0.214	0.357
Trichilia tuberculata	TRI3	12210		dry	dry	-0.380	**-0.370**	**-0.340**	-0.430	-0.295	-0.430	-0.290	0.285	0.265	0.288	0.238	0.331	0.235	0.350
Triplaris cumingiana	TRIC	400	dry	dry	dry	-0.390	-0.430	-0.280	-0.555	-0.215	-0.611	-0.180	0.252	0.228	0.335	0.177	0.397	0.172	0.368
Trophis caucana	OLMA	216	wet	wet	wet	-0.180	**-0.450**	**-0.280**	**-0.555**	**-0.200**	**-0.620**	**-0.185**	0.169	**0.224**	**0.337**	**0.178**	**0.388**	**0.169**	**0.384**
Virola sebifera	VIR1	285	wet	wet	wet	-0.315	-0.441	-0.280	-0.480	-0.280	-0.495	-0.270	0.265	0.224	0.341	0.215	0.344	0.220	0.335

Table S5 Species-specific mean estimates of log growth rates (β0) and growth responses to SWP (β1) and height (β2) and their 95% credible intervals (CI) for all 53 species in the model with growth > 0 (presented in the main text). Estimates are significant when the 95% CI did not include zero. Underlined estimates indicate signficant estimates of β0 and β2, bold and underlined underlined estimates indicate significant estimates of β1. The 4-letter mnemonics (i.e. species codes) are used to indicate species in Fig. 1 and Figs. S1.2, S1.6 and S1.8.

	Species	Sample	Constant (β0)			Moisture response (β1)			Height response (β2)		
Species	code	size (*n*)	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+
Acalypha diversifolia	ACAD	193	-1.893	-1.732	-1.576	-0.508	0.039	0.570	-0.622	-0.479	-0.335
Aegiphila panamensis	AEGP	118	-1.685	-1.500	-1.315	**-1.470**	**-0.822**	**-0.174**	-0.936	-0.749	-0.561
Alseis blackiana	ALSB	570	-2.092	-1.935	-1.770	-0.261	0.286	0.825	-0.893	-0.767	-0.646
Beilschmiedia pendula	BEIP	2127	-2.483	-2.356	-2.227	-0.121	0.131	0.380	-0.663	-0.538	-0.412
Brosimum alicastrum	BROA	174	-2.130	-1.881	-1.636	-0.571	-0.023	0.507	-0.956	-0.718	-0.476
Capparis frondosa	CAPF	1533	-2.184	-2.092	-1.998	-0.123	0.093	0.306	-1.153	-1.055	-0.958
Cassipourea elliptica	CAS3	205	-2.128	-1.965	-1.801	-0.922	-0.216	0.467	-0.832	-0.685	-0.538
Chrysophyllum argenteum	CHRA	151	-2.272	-2.052	-1.824	-0.745	-0.211	0.343	-0.935	-0.713	-0.507
Chrysophyllum cainito	CHRC	465	-2.288	-2.174	-2.058	-0.621	-0.271	0.086	-0.957	-0.794	-0.633
Cinnamomum triplinerve	PHOM	134	-2.255	-2.052	-1.848	-0.662	-0.033	0.594	-0.753	-0.497	-0.237
Cordia lasiocalyx	CORL	167	-1.872	-1.654	-1.435	-0.382	0.140	0.665	-0.864	-0.660	-0.454
Coussarea curvigemmia	COUC	186	-2.323	-2.174	-2.023	-0.191	0.293	0.779	-0.669	-0.479	-0.294
Desmopsis panamensis	DESP	784	-2.028	-1.937	-1.847	-0.169	0.079	0.325	-0.624	-0.535	-0.448
Drypetes standleyi	DRYS	236	-1.855	-1.659	-1.464	-0.205	0.241	0.684	-0.766	-0.594	-0.421
Erythroxylum macrophyllum	ERYM	114	-2.292	-2.077	-1.857	-1.295	-0.414	0.469	-0.767	-0.506	-0.243
Eugenia galalonensis	EUGG	267	-2.011	-1.867	-1.719	-0.284	0.203	0.709	-0.620	-0.486	-0.358
Eugenia nesiotica	EUGN	104	-2.034	-1.721	-1.406	-1.205	-0.168	0.757	-1.026	-0.804	-0.586
Eugenia oerstediana	EUGO	1978	-1.825	-1.750	-1.675	-0.113	0.097	0.306	-0.803	-0.736	-0.670
Faramea occidentalis	FARO	9362	-2.296	-2.238	-2.180	-0.156	-0.054	0.047	-0.712	-0.672	-0.631
Garcinia intermedia	RHEE	509	-2.552	-2.423	-2.293	-0.293	0.055	0.411	-0.397	-0.278	-0.159
Guapira standleyana	GUAS	129	-1.812	-1.654	-1.498	-0.629	-0.107	0.401	-1.069	-0.843	-0.616
Guarea guidonia	GUA2	391	-2.280	-2.153	-2.026	-0.335	0.063	0.458	-0.732	-0.586	-0.440
Gustavia superba	GUSS	479	-2.455	-2.333	-2.208	-0.313	0.107	0.534	-0.803	-0.645	-0.494
Heisteria acuminata	HEIA	117	-2.281	-2.061	-1.847	-0.306	0.298	0.904	-1.106	-0.870	-0.645
Heisteria concinna	HEIC	735	-2.186	-2.097	-2.004	-0.357	-0.131	0.102	-0.652	-0.517	-0.383
Hirtella triandra	HIRT	297	-1.716	-1.558	-1.400	-0.408	-0.032	0.336	-0.885	-0.731	-0.580
Hybanthus prunifolius	HYBP	6265	-2.092	-2.032	-1.971	-0.122	0.012	0.147	-0.706	-0.667	-0.629

Inga marginata	INMA	1478	-2.004	-1.916	-1.829	-0.223	0.016	0.262	-0.583	-0.498	-0.414
Mouriri myrtilloides	MOUM	1492	-1.668	-1.573	-1.479	-0.133	0.068	0.270	-0.714	-0.643	-0.572
Nectandra lineata	NECL	236	-2.174	-1.977	-1.777	-0.182	0.349	0.862	-0.564	-0.369	-0.173
Ocotea puberula	OCOP	139	-2.108	-1.947	-1.782	-0.171	0.227	0.616	-0.877	-0.678	-0.481
Ouratea lucens	OURL	179	-2.518	-2.318	-2.124	-0.719	-0.190	0.321	-0.932	-0.728	-0.528
Picramnia latifolia	PICL	245	-2.037	-1.873	-1.707	-0.254	0.234	0.711	-0.752	-0.602	-0.453
Piper darienense	PPDA	178	-2.015	-1.872	-1.730	-0.408	0.026	0.475	-0.917	-0.748	-0.584
Pouteria reticulata	POUU	636	-2.317	-2.178	-2.035	**-0.743**	**-0.399**	**-0.060**	-0.698	-0.535	-0.372
Protium tenuifolium	PROT	331	-1.926	-1.755	-1.582	-0.128	0.352	0.830	-0.867	-0.725	-0.591
Psychotria hoffmannseggiana	PYFU	399	-1.284	-1.171	-1.057	-0.292	0.040	0.369	-0.611	-0.529	-0.448
Psychotria horizontalis	PYHO	1445	-2.040	-1.965	-1.889	**0.010**	**0.215**	**0.424**	-0.835	-0.772	-0.710
Psychotria marginata	PYMA	209	-1.919	-1.745	-1.576	-0.536	0.107	0.750	-0.724	-0.593	-0.464
Psychotria racemosa	PYRA	123	-1.632	-1.405	-1.179	**-1.620**	**-0.922**	**-0.230**	-0.785	-0.612	-0.439
Quararibea asterolepis	QUA1	2156	-2.030	-1.951	-1.872	-0.043	0.159	0.355	-0.870	-0.787	-0.704
Randia armata	RANA	4033	-2.297	-2.236	-2.172	-0.134	0.006	0.148	-1.098	-1.031	-0.966
Rinorea sylvatica	RIN2	344	-2.162	-2.027	-1.894	-0.790	-0.304	0.197	-0.780	-0.644	-0.507
Simarouba amara	SIMA	169	-1.849	-1.622	-1.398	-0.060	0.461	0.981	-0.710	-0.523	-0.338
Sorocea affinis	SORA	957	-1.977	-1.893	-1.810	-0.240	0.008	0.249	-0.816	-0.711	-0.605
Stylogyne turbacensis	STYS	279	-2.360	-2.228	-2.096	-0.403	-0.012	0.379	-0.974	-0.812	-0.655
Swartzia simplex var.grandiflora	SWA1	268	-2.075	-1.866	-1.655	-0.477	-0.004	0.463	-1.064	-0.869	-0.677
Tabebuia rosea	TABR	113	-1.759	-1.548	-1.337	-0.483	0.128	0.732	-0.812	-0.619	-0.420
Tabernaemontana arborea	TABA	110	-2.318	-2.034	-1.746	-0.243	0.797	1.734	-0.918	-0.706	-0.499
Tetragastris panamensis	TET2	1024	-2.137	-2.027	-1.917	-0.454	-0.227	0.000	-0.669	-0.563	-0.458
Trichilia tuberculata	TRI3	6275	-2.345	-2.285	-2.225	-0.164	-0.050	0.064	-0.669	-0.623	-0.577
Triplaris cumingiana	TRIC	179	-2.291	-2.142	-1.992	-0.791	-0.255	0.273	-1.018	-0.781	-0.551
Virola sebifera	VIR1	114	-2.152	-1.945	-1.736	-0.217	0.444	1.123	-0.769	-0.515	-0.245

Table S6 Species-specific mean estimates of mortality rates (β0) and mortality responses to SWP (β1) and height (β2) and their 95% credible intervals (CI) for all 43 species in the model (presented in the main text). Estimates are significant when the 95% CI did not include zero. Underlined estimates indicate signficant estimates of β0 and β2, bold and underlined underlined estimates indicate significant estimates of β1. The 4-letter mnemonics (i.e. species codes) are used to indicate species in Fig. 1 and Figs. S1.2, S1.6 and S1.8.

	Species	Sample	Constant (β0)			Moisture response (β1)			Height response (β2)		
Species	**code**	**size (*n*)**	**CI-**	**mean**	**CI+**	**CI-**	**mean**	**CI+**	**CI-**	**mean**	**CI+**
Acalypha diversifolia	ACAD	104	-1.805	-1.171	-0.545	**-2.848**	**-1.395**	**-0.096**	-1.812	-1.272	-0.712
Aegiphila panamensis	AEGP	172	-0.200	0.266	0.738	-0.704	0.752	2.203	-2.495	-1.771	-1.108
Apeiba membranacea	APEM	119	0.378	1.073	1.792	-2.205	-0.205	1.464	-2.396	-1.697	-1.067
Beilschmiedia pendula	BEIP	1783	0.884	1.165	1.451	**-1.165**	**-0.644**	**-0.092**	-1.948	-1.608	-1.277
Capparis frondosa	CAPF	218	-1.513	-1.158	-0.807	-1.477	-0.262	0.957	-2.187	-1.574	-0.976
Cecropia insignis	CECI	166	0.940	1.411	1.901	-0.948	0.684	2.177	-1.614	-1.098	-0.576
Chrysophyllum cainito	CHRC	220	-0.750	-0.427	-0.110	**0.195**	**1.380**	**2.565**	-1.795	-1.121	-0.387
Cinnamomum triplinerve	PHOM	101	0.046	0.464	0.882	-1.303	0.296	1.778	-2.079	-1.340	-0.543
Coussarea curvigemmia	COUC	129	-0.388	0.034	0.452	-1.644	-0.391	0.804	-2.134	-1.382	-0.597
Dendropanax arboreus	DENA	180	-0.300	0.482	1.260	-2.368	-0.595	1.071	-2.341	-1.635	-0.957
Desmopsis panamensis	DESP	333	-1.369	-1.007	-0.646	-0.869	0.111	1.092	-2.344	-1.752	-1.198
Eugenia oerstediana	EUGO	836	-0.818	-0.600	-0.387	-0.539	0.062	0.669	-1.803	-1.367	-0.938
Faramea occidentalis	FARO	6112	-0.280	-0.151	-0.023	**-0.638**	**-0.360**	**-0.081**	-1.746	-1.575	-1.409
Guapira standleyana	GUAS	164	-0.002	0.370	0.756	-0.632	0.558	1.745	-1.441	-0.805	-0.102
Guarea guidonia	GUA2	178	-0.624	-0.288	0.039	**-2.711**	**-1.487**	**-0.342**	-2.152	-1.450	-0.717
Gustavia superba	GUSS	348	-0.344	-0.083	0.179	-0.954	0.006	0.974	-1.669	-1.216	-0.760
Hampea appendiculata	HAM2	100	0.268	0.814	1.368	-2.815	-0.512	1.793	-2.574	-1.739	-0.973
Heisteria concinna	HEIC	487	-0.563	-0.333	-0.111	-0.024	0.646	1.333	-1.892	-1.332	-0.753
Hirtella triandra	HIRT	214	0.069	0.393	0.718	-1.213	-0.127	0.946	-2.637	-1.964	-1.362
Hybanthus prunifolius	HYBP	5661	-0.727	-0.561	-0.394	-0.214	0.096	0.412	-2.133	-1.939	-1.747
Inga marginata	INMA	567	-0.965	-0.749	-0.537	-1.293	-0.565	0.165	-2.012	-1.489	-0.974
Jacaranda copaia	JACC	159	1.432	2.251	3.165	-2.235	1.198	5.174	-2.491	-1.707	-0.988
Miconia argentea	MIC2	115	-0.291	0.261	0.817	-2.585	-0.784	0.764	-1.720	-1.234	-0.765
Mouriri myrtilloides	MOUM	488	-0.477	-0.254	-0.032	-0.865	-0.183	0.501	-2.988	-2.312	-1.700
Ocotea puberula	OCOP	232	0.018	0.362	0.714	-0.351	0.661	1.650	-2.220	-1.499	-0.741
Piper reticulatum	PPRE	151	-0.497	0.238	0.990	-2.221	-0.256	1.725	-1.690	-1.122	-0.538
Pouteria reticulata	POUU	331	0.042	0.385	0.730	-1.416	-0.490	0.425	-2.316	-1.632	-0.982

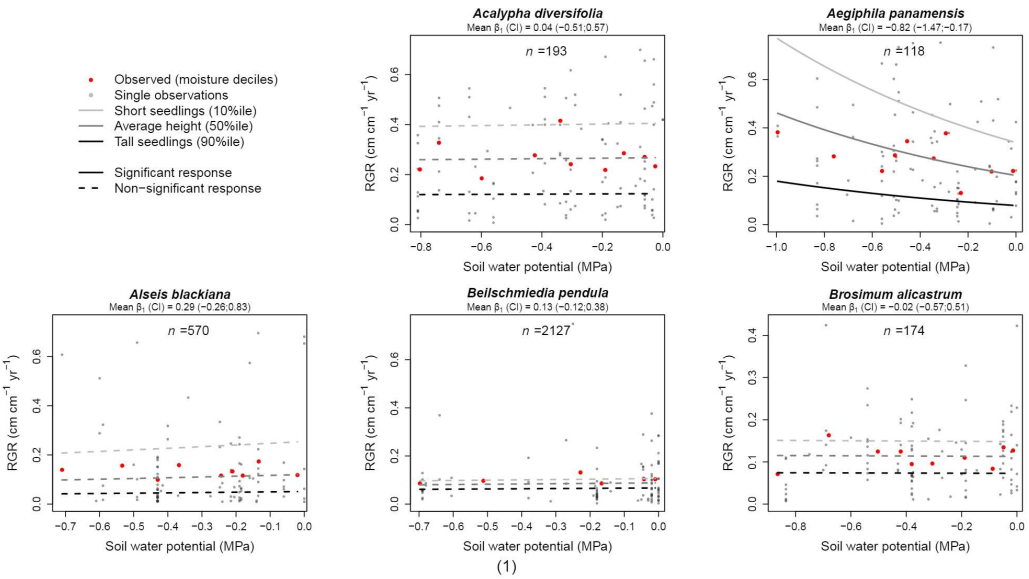
Protium tenuifolium	PROT	117	-0.464	-0.025	0.400	-2.188	-0.577	1.054	-2.181	-1.397	-0.587
Psychotria hoffmannseggiana	PYFU	345	-0.890	-0.507	-0.129	-1.027	-0.137	0.743	-2.017	-1.550	-1.099
Psychotria horizontalis	PYHO	1316	-1.155	-0.820	-0.497	-0.903	-0.389	0.129	-1.700	-1.413	-1.131
Psychotria marginata	PYMA	191	-1.264	-0.602	0.069	-1.688	-0.197	1.250	-1.915	-1.383	-0.843
Quararibea asterolepis	QUA1	1299	-0.070	0.097	0.262	-0.111	0.402	0.910	-1.960	-1.636	-1.316
Randia armata	RANA	2473	-0.545	-0.366	-0.189	-0.382	0.017	0.414	-1.887	-1.599	-1.311
Rinorea sylvatica	RIN2	183	-1.247	-0.736	-0.228	-1.220	0.314	1.814	-2.406	-1.711	-1.073
Senna dariensis	SEND	178	0.162	0.700	1.243	-3.453	-1.221	0.884	-2.622	-1.834	-1.155
Sorocea affinis	SORA	604	-0.403	-0.144	0.112	-0.491	0.145	0.791	-1.844	-1.363	-0.887
Stylogyne turbacensis	STYS	137	-1.603	-0.991	-0.342	-1.176	-0.068	1.074	-1.770	-1.139	-0.454
Tabebuia rosea	TABR	133	0.151	0.533	0.928	-0.859	0.304	1.478	-2.763	-1.954	-1.250
Tetragastris panamensis	TET2	570	0.406	0.697	0.996	-0.251	0.445	1.151	-2.397	-1.792	-1.220
Trichilia tuberculata	TRI3	3660	-0.565	-0.411	-0.261	-0.553	-0.224	0.096	-2.116	-1.856	-1.606
Triplaris cumingiana	TRIC	151	-0.982	-0.506	-0.030	-1.152	0.293	1.712	-2.489	-1.730	-1.021
Trophis caucana	OLMA	101	0.153	0.758	1.390	-2.854	-0.535	1.910	-1.832	-1.154	-0.363
Virola sebifera	VIR1	120	0.098	0.491	0.893	-2.048	-0.586	0.831	-2.475	-1.703	-0.985

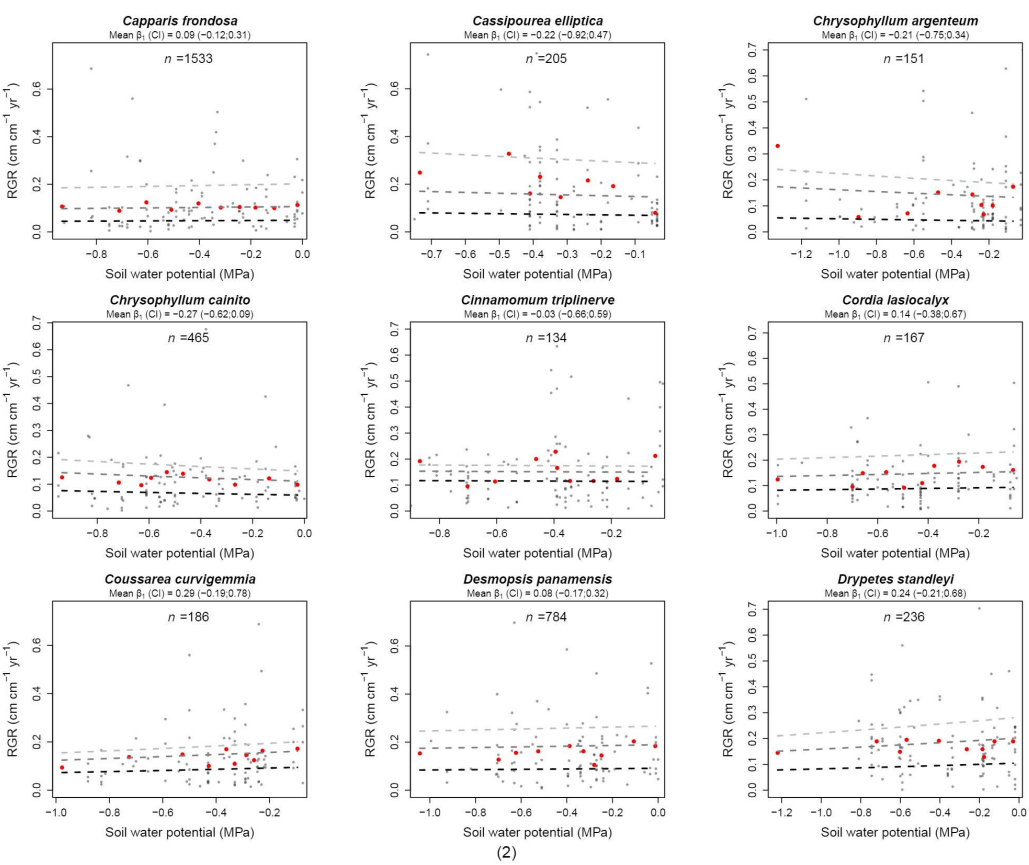
Table S7 Species-specific mean estimates of growth rates (β0) and growth responses to SWP (β1) and height (β2) and their 95% credible intervals (CI) for all 53 species in the model including growth ≤ 0 (presented in Appendix S3). Estimates are significant when the 95% CI did not include zero. Underlined estimates indicate signficant estimates of β0 and β2, bold and underlined underlined estimates indicate significant estimates of β1. The 4-letter mnemonics (i.e. species codes) are used to indicate species in Fig. 1 and Figs. S1.2, S1.6 and S1.8.

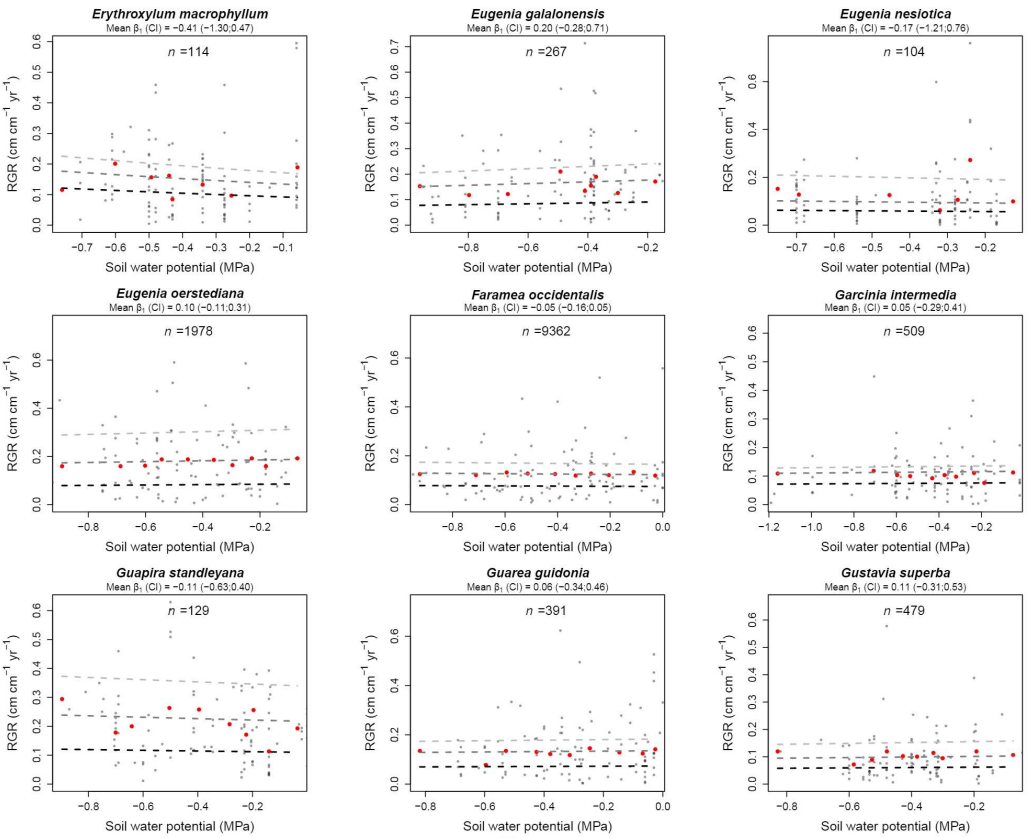
	Species	Sample	Constant (β0)			Moisture response (β1)			Height response (β2)		
Species	code	size (*n*)	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+
Acalypha diversifolia	ACAD	229	0.298	0.336	0.375	-0.121	0.017	0.157	-0.128	-0.091	-0.056
Aegiphila panamensis	AEGP	130	0.384	0.426	0.470	-0.315	-0.156	0.006	-0.209	-0.166	-0.123
Alseis blackiana	ALSB	687	0.286	0.318	0.352	-0.084	0.032	0.148	-0.145	-0.120	-0.096
Beilschmiedia pendula	BEIP	2669	0.185	0.209	0.232	-0.026	0.017	0.060	-0.093	-0.071	-0.048
Brosimum alicastrum	BROA	202	0.280	0.331	0.382	-0.163	-0.056	0.051	-0.182	-0.132	-0.083
Capparis frondosa	CAPF	1995	0.238	0.256	0.274	-0.023	0.018	0.060	-0.172	-0.151	-0.131
Cassipourea elliptica	CAS3	232	0.294	0.330	0.367	-0.232	-0.068	0.100	-0.178	-0.144	-0.111
Chrysophyllum argenteum	CHRA	171	0.231	0.275	0.320	-0.176	-0.071	0.038	-0.134	-0.091	-0.047
Chrysophyllum cainito	CHRC	541	0.237	0.259	0.280	**-0.137**	**-0.070**	**-0.003**	-0.154	-0.122	-0.092
Cinnamomum triplinerve	PHOM	147	0.246	0.290	0.333	-0.132	0.002	0.140	-0.118	-0.063	-0.005
Cordia lasiocalyx	CORL	177	0.340	0.383	0.426	-0.058	0.046	0.149	-0.166	-0.125	-0.085
Coussarea curvigemmia	COUC	210	0.229	0.259	0.290	-0.068	0.041	0.152	-0.131	-0.090	-0.051
Desmopsis panamensis	DESP	893	0.282	0.301	0.321	-0.068	-0.013	0.043	-0.109	-0.089	-0.070
Drypetes standleyi	DRYS	278	0.316	0.356	0.396	-0.050	0.043	0.133	-0.140	-0.106	-0.071
Erythroxylum macrophyllum	ERYM	146	0.209	0.254	0.301	-0.361	-0.158	0.041	-0.155	-0.100	-0.047
Eugenia galalonensis	EUGG	306	0.283	0.313	0.345	-0.109	0.001	0.109	-0.118	-0.088	-0.060
Eugenia nesiotica	EUGN	134	0.306	0.372	0.439	-0.209	0.001	0.210	-0.198	-0.151	-0.104
Eugenia oerstediana	EUGO	2265	0.336	0.351	0.366	-0.027	0.017	0.062	-0.160	-0.145	-0.129
Faramea occidentalis	FARO	10980	0.228	0.239	0.250	-0.030	-0.009	0.012	-0.113	-0.105	-0.096
Garcinia intermedia	RHEE	682	0.161	0.184	0.208	-0.069	-0.007	0.058	-0.050	-0.028	-0.007
Guapira standleyana	GUAS	149	0.298	0.336	0.374	**-0.337**	**-0.198**	**-0.065**	-0.211	-0.154	-0.099
Guarea guidonia	GUA2	462	0.222	0.247	0.272	-0.081	0.007	0.092	-0.125	-0.093	-0.061
Gustavia superba	GUSS	650	0.166	0.189	0.213	-0.011	0.065	0.141	-0.109	-0.078	-0.049
Heisteria acuminata	HEIA	139	0.245	0.289	0.333	-0.102	0.026	0.153	-0.199	-0.148	-0.101
Heisteria concinna	HEIC	897	0.227	0.247	0.267	-0.037	0.018	0.070	-0.118	-0.086	-0.055
Hirtella triandra	HIRT	329	0.368	0.403	0.437	-0.074	0.004	0.081	-0.177	-0.144	-0.112
Hybanthus prunifolius	HYBP	7384	0.265	0.277	0.289	-0.022	0.008	0.038	-0.135	-0.126	-0.117

Inga marginata	INMA	1757	0.282	0.300	0.318	-0.025	0.028	0.082	-0.112	-0.094	-0.076
Mouriri myrtilloides	MOUM	1792	0.340	0.360	0.379	-0.057	-0.015	0.028	-0.134	-0.118	-0.103
Nectandra lineata	NECL	264	0.266	0.308	0.351	-0.077	0.033	0.141	-0.100	-0.059	-0.018
Ocotea puberula	OCOP	160	0.243	0.280	0.317	-0.077	0.018	0.114	-0.138	-0.092	-0.047
Ouratea lucens	OURL	222	0.186	0.227	0.268	-0.145	-0.033	0.077	-0.154	-0.113	-0.071
Picramnia latifolia	PICL	271	0.287	0.320	0.354	-0.013	0.087	0.185	-0.136	-0.104	-0.073
Piper darienense	PPDA	218	0.248	0.285	0.323	-0.173	-0.054	0.072	-0.180	-0.134	-0.090
Pouteria reticulata	POUU	715	0.233	0.258	0.284	-0.092	-0.034	0.026	-0.107	-0.076	-0.046
Protium tenuifolium	PROT	357	0.314	0.347	0.380	-0.039	0.056	0.150	-0.128	-0.102	-0.076
Psychotria hoffmannseggiana	PYFU	421	0.492	0.519	0.545	-0.078	0.005	0.088	-0.156	-0.136	-0.116
Psychotria horizontalis	PYHO	1709	0.270	0.287	0.304	-0.009	0.046	0.100	-0.193	-0.176	-0.159
Psychotria marginata	PYMA	227	0.330	0.365	0.400	-0.162	-0.017	0.135	-0.149	-0.119	-0.089
Psychotria racemosa	PYRA	128	0.384	0.437	0.491	**-0.442**	**-0.265**	**-0.087**	-0.170	-0.128	-0.086
Quararibea asterolepis	QUA1	2652	0.278	0.294	0.309	-0.009	0.031	0.071	-0.165	-0.148	-0.132
Randia armata	RANA	5024	0.221	0.233	0.246	-0.030	0.001	0.031	-0.230	-0.214	-0.198
Rinorea sylvatica	RIN2	423	0.253	0.281	0.309	-0.101	0.006	0.111	-0.151	-0.122	-0.094
Simarouba amara	SIMA	173	0.357	0.402	0.448	**0.001**	**0.102**	**0.203**	-0.136	-0.096	-0.058
Sorocea affinis	SORA	1113	0.291	0.309	0.327	-0.063	-0.010	0.044	-0.169	-0.145	-0.121
Stylogyne turbacensis	STYS	364	0.187	0.216	0.245	-0.145	-0.051	0.042	-0.174	-0.137	-0.101
Swartzia simplex var.grandiflora	SWA1	350	0.244	0.288	0.333	-0.085	0.010	0.107	-0.186	-0.142	-0.100
Tabebuia rosea	TABR	125	0.341	0.388	0.435	-0.057	0.077	0.213	-0.146	-0.101	-0.055
Tabernaemontana arborea	TABA	123	0.265	0.323	0.379	-0.100	0.109	0.304	-0.152	-0.111	-0.069
Tetragastris panamensis	TET2	1109	0.263	0.283	0.302	**-0.083**	**-0.041**	**0.000**	-0.087	-0.068	-0.050
Trichilia tuberculata	TRI3	7381	0.214	0.225	0.237	-0.037	-0.013	0.010	-0.087	-0.077	-0.068
Triplaris cumingiana	TRIC	220	0.225	0.256	0.287	-0.093	0.030	0.155	-0.234	-0.177	-0.123
Virola sebifera	VIR1	134	0.245	0.289	0.335	-0.061	0.088	0.244	-0.154	-0.097	-0.039

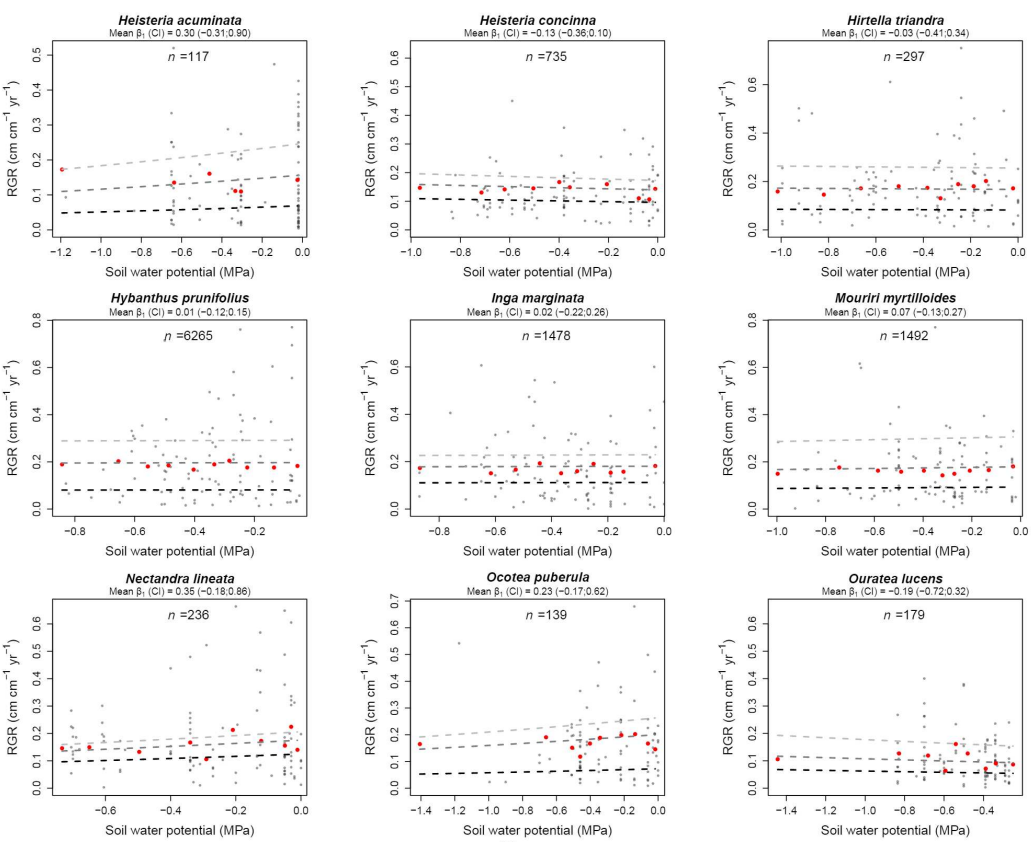
Figure S4 Responses of relative growth rates (RGR) to dry−season soil water potentials (page 1−7) and seedling height (page 8−13) for all species in the growth model with only positive growth observations (presented in the main text). Predicted responses (lines) and observed responses (dots) are shown. Growth is predicted against soil water potential for three levels of seedling height (short, average, tall), and against seedling height for three moisture levels (dry, average and wet), with levels representing the 10th, 50th and 90th percentile of the plotted species. The respective slopes of the response and their credible intervals are given above each panel. Red dots represent mean RGR for ten height or ten moisture classes, each containing 10% of the individuals of the species. Small grey dots show 100 randomly selected single observations.



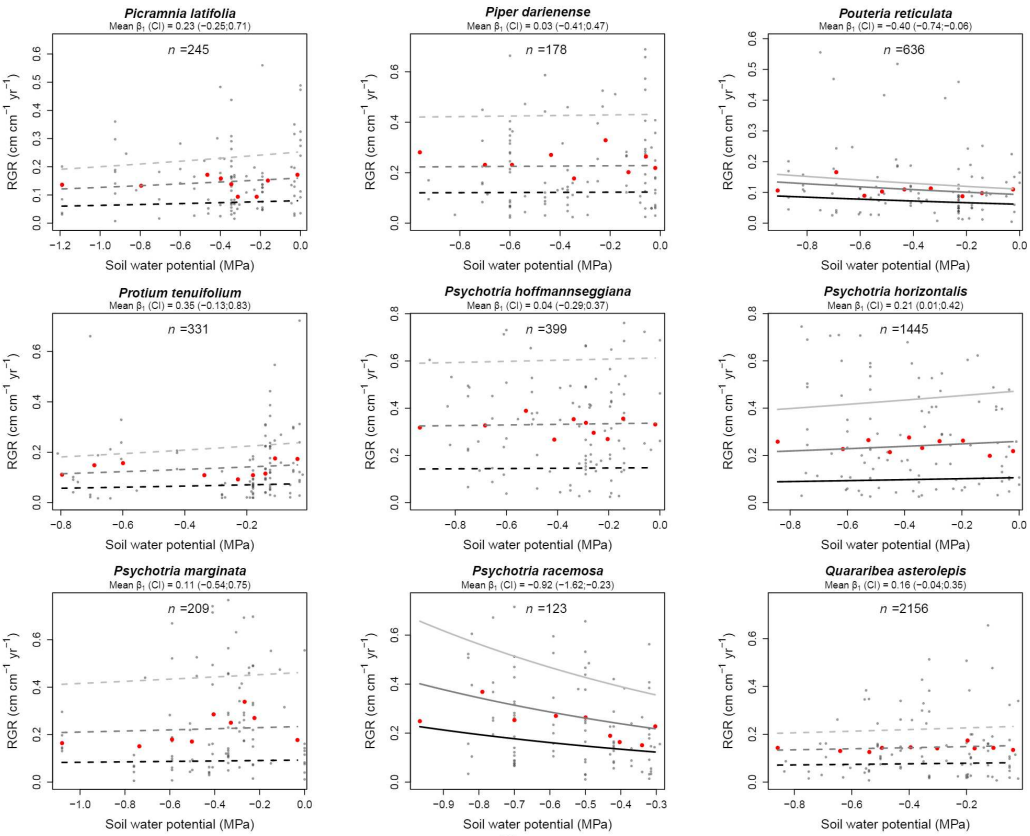



Erythroxylum macrophyllum
Mean β1 (CI) = −0.41 (−1.30;0.47)
n =114
Eugenia galalonensis
Mean β1 (CI) = 0.20 (−0.28;0.71)
n =267
Eugenia nesiotica
Mean β1 (CI) = −0.17 (−1.21;0.76)
n =104
Eugenia oerstediana
Mean β1 (CI) = 0.10 (−0.11;0.31)
n =1978
Faramea occidentalis
Mean β1 (CI) = −0.05 (−0.16;0.05)
n =9362
Garcinia intermedia
Mean β1 (CI) = 0.05 (−0.29;0.41)
n =509
Guapira standleyana
Mean β1 (CI) = −0.11 (−0.63;0.40)
n =129
Guarea guidonia
Mean β1 (CI) = 0.06 (−0.34;0.46)
n =391
Gustavia superba
Mean β1 (CI) = 0.11 (−0.31;0.53)
n =479
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

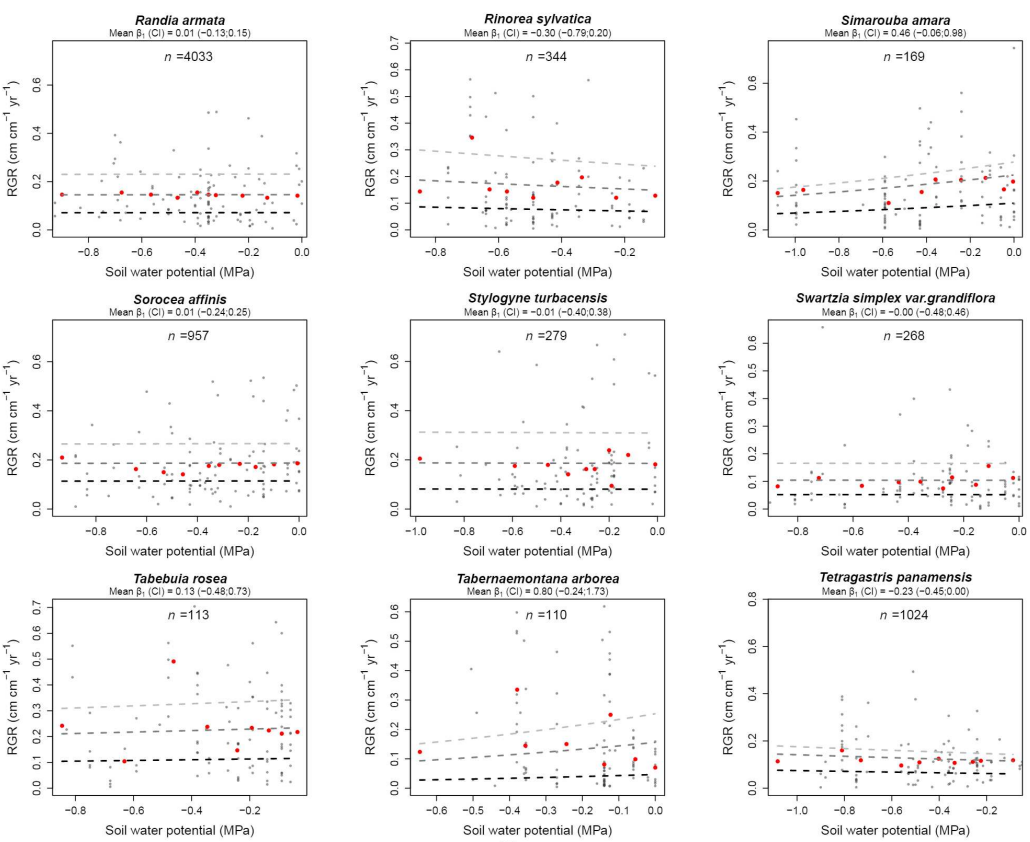
(3)


Heisteria acuminata
Mean β1 (CI) = 0.30 (−0.31;0.90)
n =117
Heisteria concinna
Mean β1 (CI) = −0.13 (−0.36;0.10)
n =735
Hirtella triandra
Mean β1 (CI) = −0.03 (−0.41;0.34)
n =297
Hybanthus prunifolius
Mean β1 (CI) = 0.01 (−0.12;0.15)
n =6265
Inga marginata
Mean β1 (CI) = 0.02 (−0.22;0.26)
n =1478
Mouriri myrtilloides
Mean β1 (CI) = 0.07 (−0.13;0.27)
n =1492
Nectandra lineata
Mean β1 (CI) = 0.35 (−0.18;0.86)
n =236
Ocotea puberula
Mean β1 (CI) = 0.23 (−0.17;0.62)
n =139
Ouratea lucens
Mean β1 (CI) = −0.19 (−0.72;0.32)
n =179
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

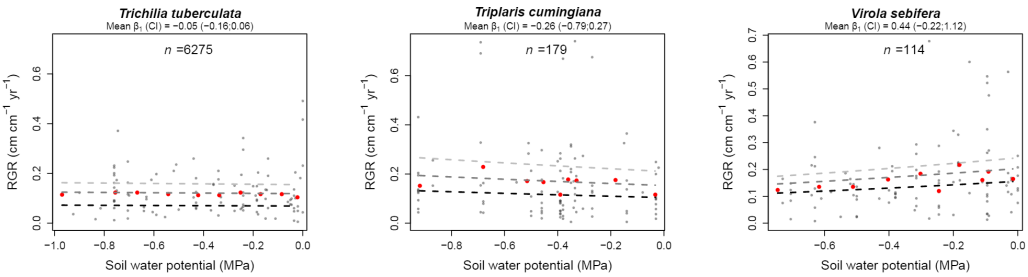
(4)


Picramnia latifolia
Mean β1 (CI) = 0.23 (−0.25;0.71)
n =245
Piper darienense
Mean β1 (CI) = 0.03 (−0.41;0.47)
n =178
Pouteria reticulata
Mean β1 (CI) = −0.40 (−0.74;−0.06)
n =636
Protium tenuifolium
Mean β1 (CI) = 0.35 (−0.13;0.83)
n =331
Psychotria hoffmannseggiana
Mean β1 (CI) = 0.04 (−0.29;0.37)
n =399
Psychotria horizontalis
Mean β1 (CI) = 0.21 (0.01;0.42)
n =1445
Psychotria marginata
Mean β1 (CI) = 0.11 (−0.54;0.75)
n =209
Psychotria racemosa
Mean β1 (CI) = −0.92 (−1.62;−0.23)
n =123
Quararibea asterolepis
Mean β1 (CI) = 0.16 (−0.04;0.35)
n =2156
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

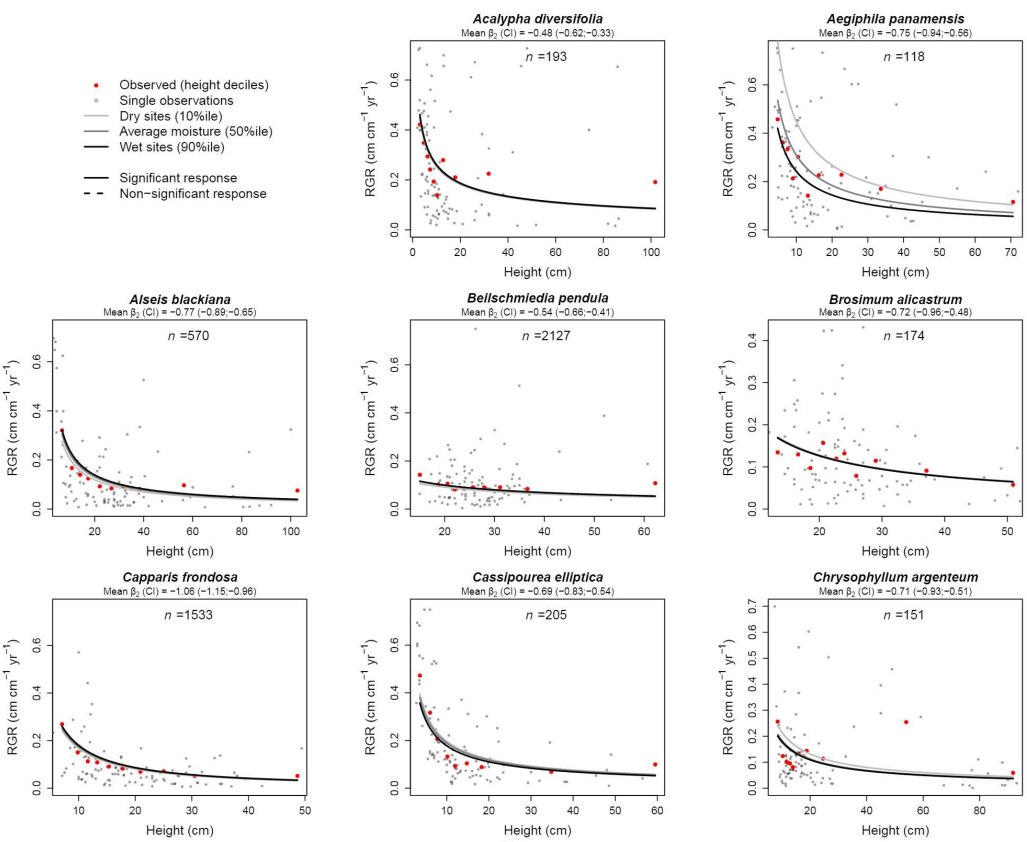
(5)


Randia armata
Mean β1 (CI) = 0.01 (−0.13;0.15)
n =4033
Rinorea sylvatica
Mean β1 (CI) = −0.30 (−0.79;0.20)
n =344
Simarouba amara
Mean β1 (CI) = 0.46 (−0.06;0.98)
n =169
Sorocea affinis
Mean β1 (CI) = 0.01 (−0.24;0.25)
n =957
Stylogyne turbacensis
Mean β1 (CI) = −0.01 (−0.40;0.38)
n =279
Swartzia simplex var.grandiflora
Mean β1 (CI) = −0.00 (−0.48;0.46)
n =268
Tabebuia rosea
Mean β1 (CI) = 0.13 (−0.48;0.73)
n =113
Tabernaemontana arborea
Mean β1 (CI) = 0.80 (−0.24;1.73)
n =110
Tetragastris panamensis
Mean β1 (CI) = −0.23 (−0.45;0.00)
n =1024
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

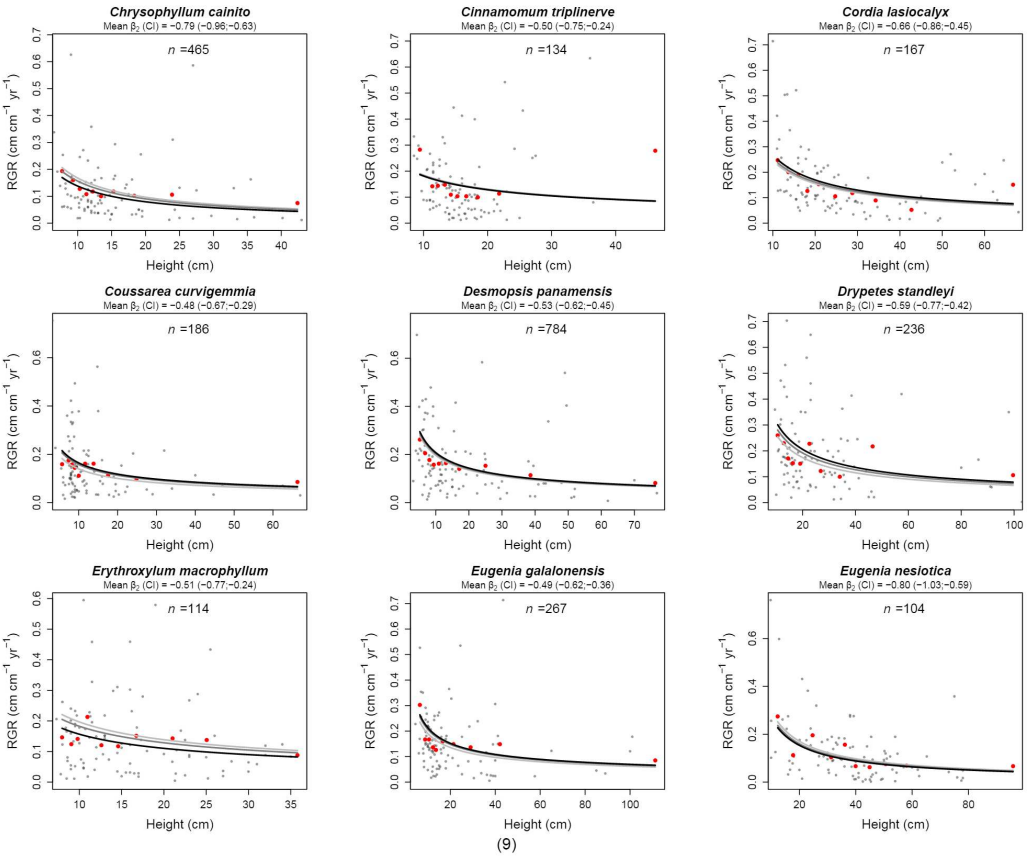
(6)


Trichilia tuberculata
Mean β1 (CI) = −0.05 (−0.16;0.06)
n =6275
Triplaris cumingiana
Mean β1 (CI) = −0.26 (−0.79;0.27)
n =179
Virola sebifera
Mean β1 (CI) = 0.44 (−0.22;1.12)
n =114
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

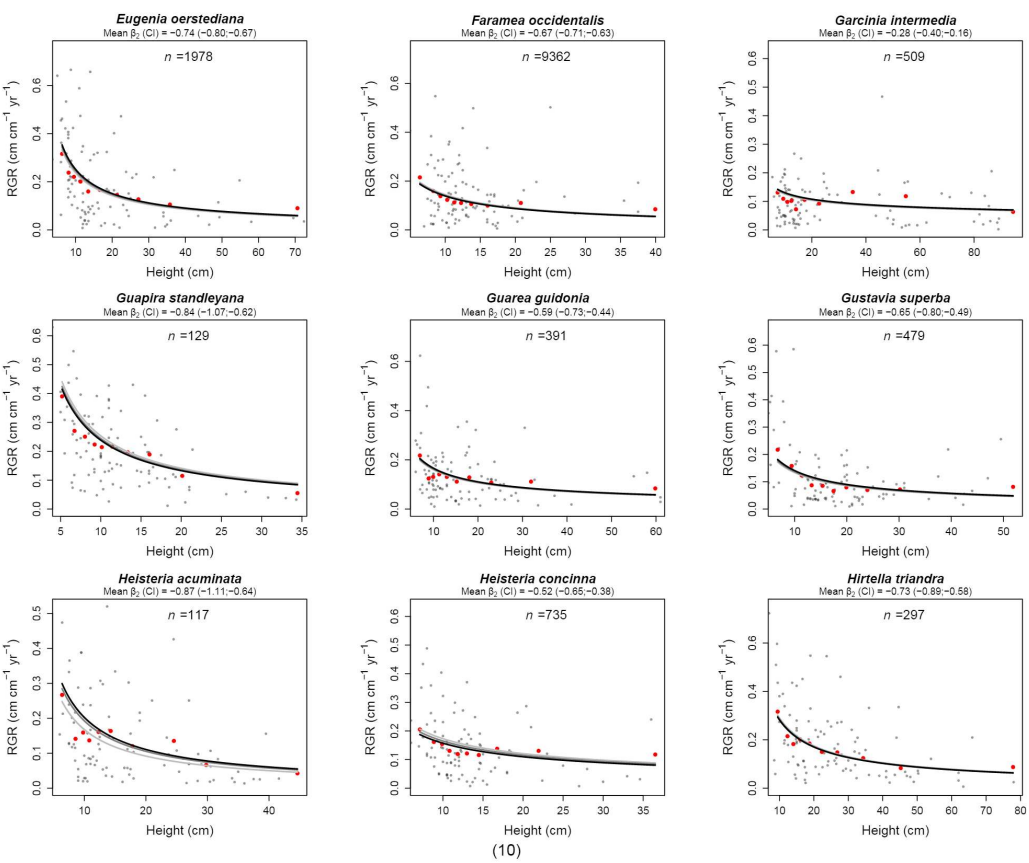
(7)


Observed (height deciles)
Single observations
Dry sites (10%ile)
Average moisture (50%ile)
Wet sites (90%ile)
Significant response
Non−significant response
Acalypha diversifolia
Mean β2 (CI) = −0.48 (−0.62;−0.33)
n =193
Aegiphila panamensis
Mean β2 (CI) = −0.75 (−0.94;−0.56)
n =118
Alseis blackiana
Mean β2 (CI) = −0.77 (−0.89;−0.65)
n =570
Beilschmiedia pendula
Mean β2 (CI) = −0.54 (−0.66;−0.41)
n =2127
Brosimum alicastrum
Mean β2 (CI) = −0.72 (−0.96;−0.48)
n =174
Capparis frondosa
Mean β2 (CI) = −1.06 (−1.15;−0.96)
n =1533
Cassipourea elliptica
Mean β2 (CI) = −0.69 (−0.83;−0.54)
n =205
Chrysophyllum argenteum
Mean β2 (CI) = −0.71 (−0.93;−0.51)
n =151
RGR (cm cm−1 yr−1)
Height (cm)

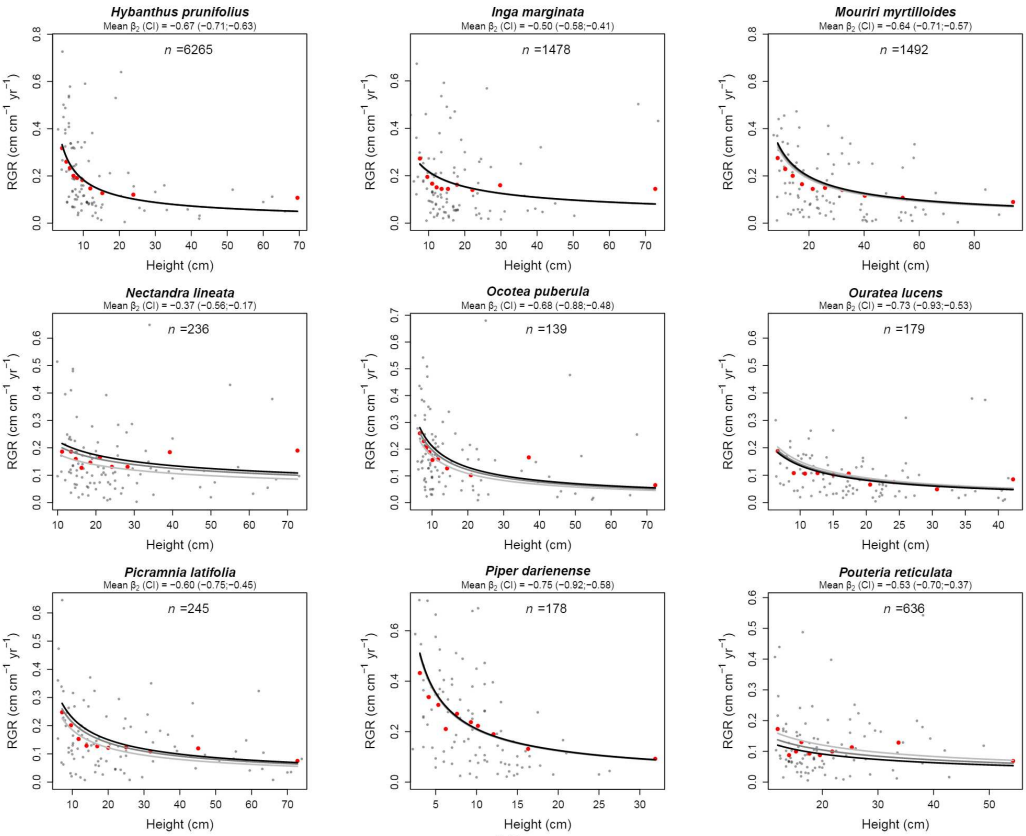
(8)


Chrysophyllum cainito
Mean β2 (CI) = −0.79 (−0.96;−0.63)
n =465
Cinnamomum triplinerve
Mean β2 (CI) = −0.50 (−0.75;−0.24)
n =134
Cordia lasiocalyx
Mean β2 (CI) = −0.66 (−0.86;−0.45)
n =167
Coussarea curvigemmia
Mean β2 (CI) = −0.48 (−0.67;−0.29)
n =186
Desmopsis panamensis
Mean β2 (CI) = −0.53 (−0.62;−0.45)
n =784
Drypetes standleyi
Mean β2 (CI) = −0.59 (−0.77;−0.42)
n =236
Erythroxylum macrophyllum
Mean β2 (CI) = −0.51 (−0.77;−0.24)
n =114
Eugenia galalonensis
Mean β2 (CI) = −0.49 (−0.62;−0.36)
n =267
Eugenia nesiotica
Mean β2 (CI) = −0.80 (−1.03;−0.59)
n =104
RGR (cm cm−1 yr−1)
Height (cm)

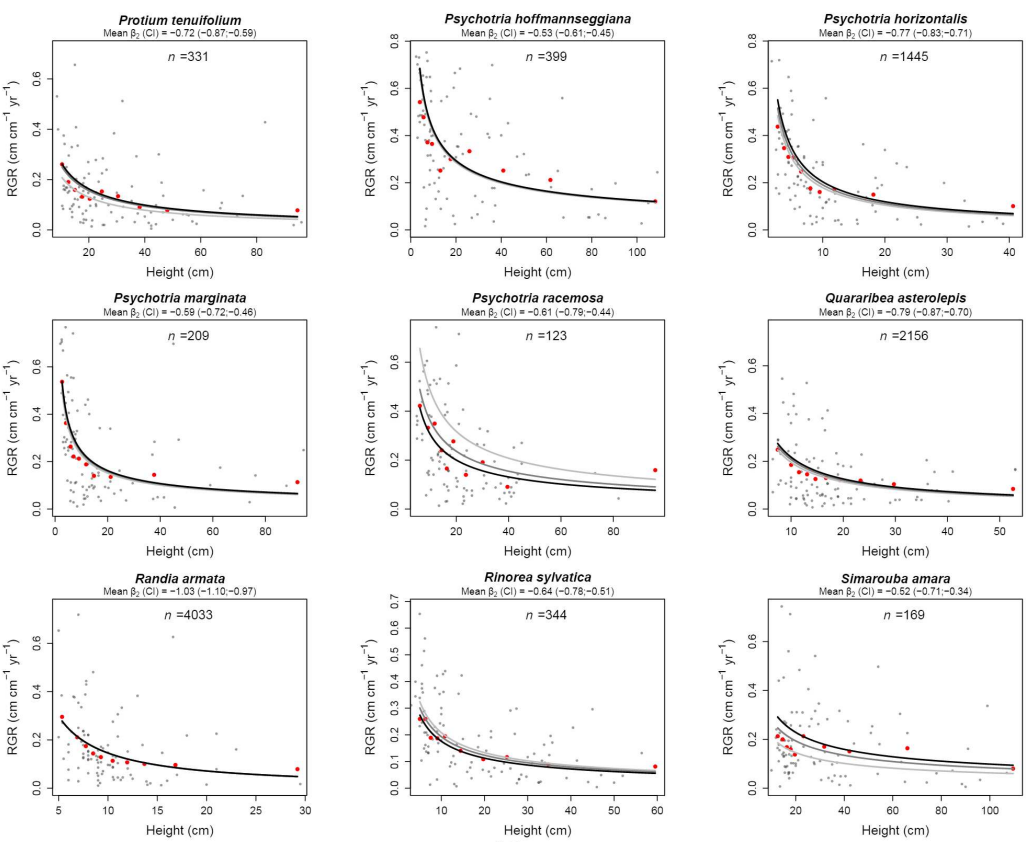
(9)


Eugenia oerstediana
Mean β2 (CI) = −0.74 (−0.80;−0.67)
n =1978
Faramea occidentalis
Mean β2 (CI) = −0.67 (−0.71;−0.63)
n =9362
Garcinia intermedia
Mean β2 (CI) = −0.28 (−0.40;−0.16)
n =509
Guapira standleyana
Mean β2 (CI) = −0.84 (−1.07;−0.62)
n =129
Guarea guidonia
Mean β2 (CI) = −0.59 (−0.73;−0.44)
n =391
Gustavia superba
Mean β2 (CI) = −0.65 (−0.80;−0.49)
n =479
Heisteria acuminata
Mean β2 (CI) = −0.87 (−1.11;−0.64)
n =117
Heisteria concinna
Mean β2 (CI) = −0.52 (−0.65;−0.38)
n =735
Hirtella triandra
Mean β2 (CI) = −0.73 (−0.89;−0.58)
n =297
RGR (cm cm−1 yr−1)
Height (cm)

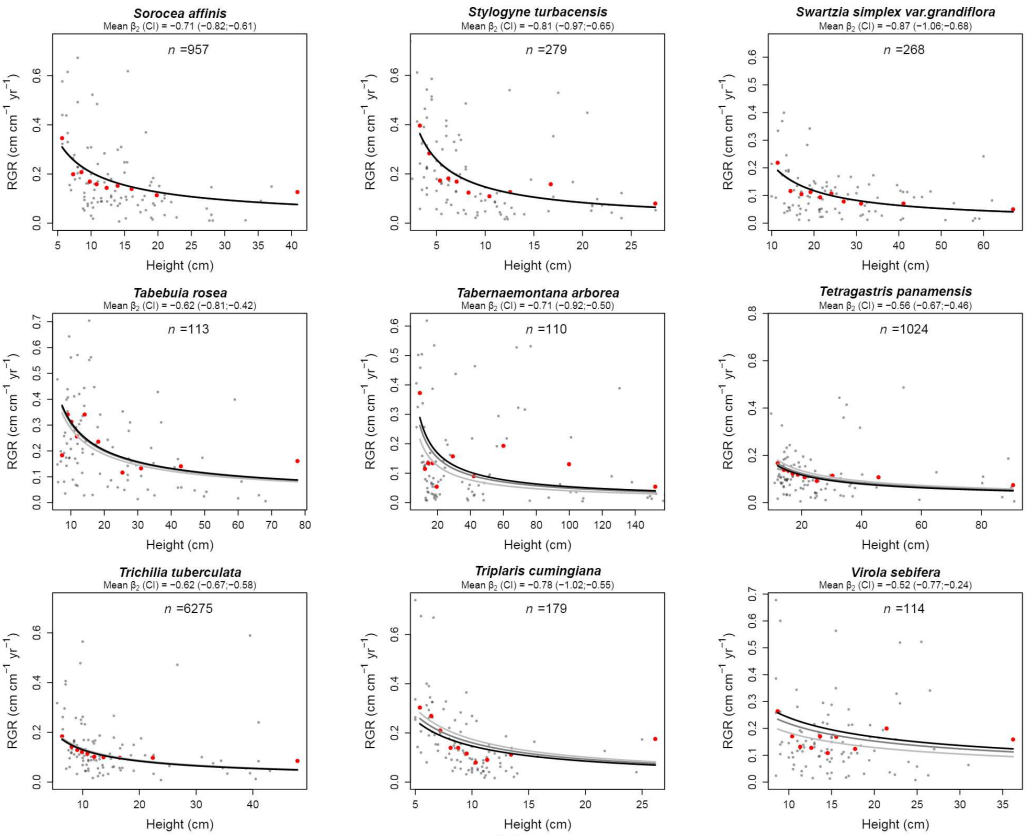
(10)


Hybanthus prunifolius
Mean β2 (CI) = −0.67 (−0.71;−0.63)
n =6265
Inga marginata
Mean β2 (CI) = −0.50 (−0.58;−0.41)
n =1478
Mouriri myrtilloides
Mean β2 (CI) = −0.64 (−0.71;−0.57)
n =1492
Nectandra lineata
Mean β2 (CI) = −0.37 (−0.56;−0.17)
n =236
Ocotea puberula
Mean β2 (CI) = −0.68 (−0.88;−0.48)
n =139
Ouratea lucens
Mean β2 (CI) = −0.73 (−0.93;−0.53)
n =179
Picramnia latifolia
Mean β2 (CI) = −0.60 (−0.75;−0.45)
n =245
Piper darienense
Mean β2 (CI) = −0.75 (−0.92;−0.58)
n =178
Pouteria reticulata
Mean β2 (CI) = −0.53 (−0.70;−0.37)
n =636
RGR (cm cm−1 yr−1)
Height (cm)

(11)

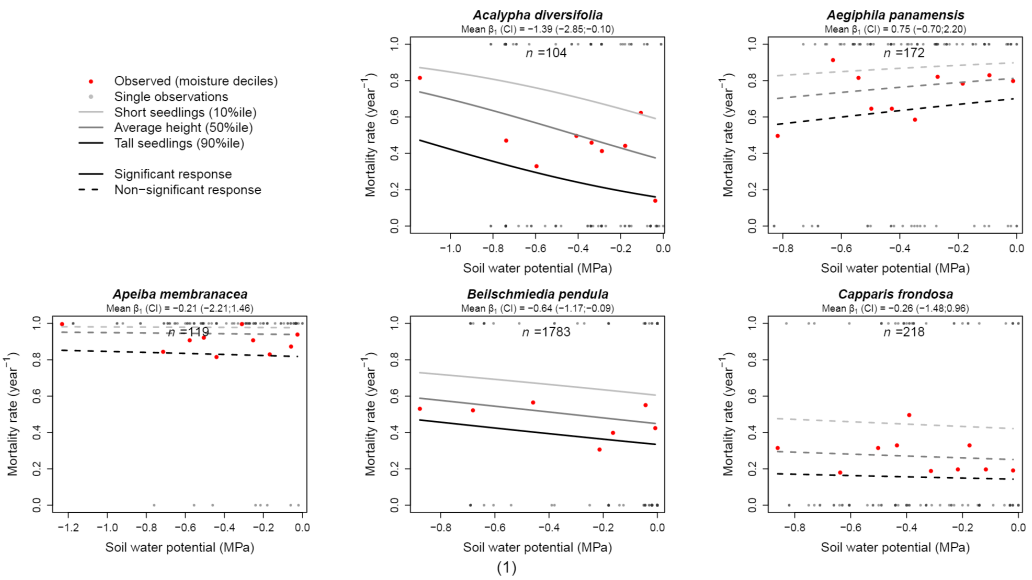

Protium tenuifolium
Mean β2 (CI) = −0.72 (−0.87;−0.59)
n =331
Psychotria hoffmannseggiana
Mean β2 (CI) = −0.53 (−0.61;−0.45)
n =399
Psychotria horizontalis
Mean β2 (CI) = −0.77 (−0.83;−0.71)
n =1445
Psychotria marginata
Mean β2 (CI) = −0.59 (−0.72;−0.46)
n =209
Psychotria racemosa
Mean β2 (CI) = −0.61 (−0.79;−0.44)
n =123
Quararibea asterolepis
Mean β2 (CI) = −0.79 (−0.87;−0.70)
n =2156
Randia armata
Mean β2 (CI) = −1.03 (−1.10;−0.97)
n =4033
Rinorea sylvatica
Mean β2 (CI) = −0.64 (−0.78;−0.51)
n =344
Simarouba amara
Mean β2 (CI) = −0.52 (−0.71;−0.34)
n =169
RGR (cm cm−1 yr−1)
Height (cm)

(12)

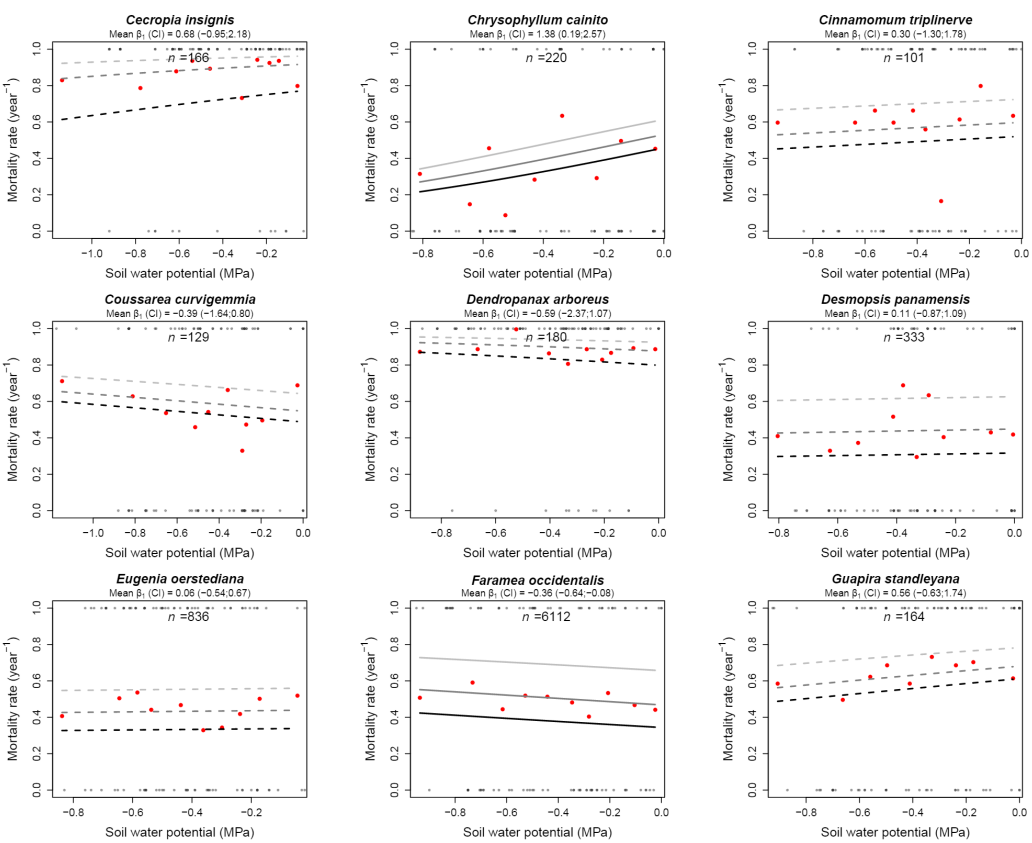

Sorocea affinis
Mean β2 (CI) = −0.71 (−0.82;−0.61)
n =957
Stylogyne turbacensis
Mean β2 (CI) = −0.81 (−0.97;−0.65)
n =279
Swartzia simplex var.grandiflora
Mean β2 (CI) = −0.87 (−1.06;−0.68)
n =268
Tabebuia rosea
Mean β2 (CI) = −0.62 (−0.81;−0.42)
n =113
Tabernaemontana arborea
Mean β2 (CI) = −0.71 (−0.92;−0.50)
n =110
Tetragastris panamensis
Mean β2 (CI) = −0.56 (−0.67;−0.46)
n =1024
Trichilia tuberculata
Mean β2 (CI) = −0.62 (−0.67;−0.58)
n =6275
Triplaris cumingiana
Mean β2 (CI) = −0.78 (−1.02;−0.55)
n =179
Virola sebifera
Mean β2 (CI) = −0.52 (−0.77;−0.24)
n =114
RGR (cm cm−1 yr−1)
Height (cm)

(13)

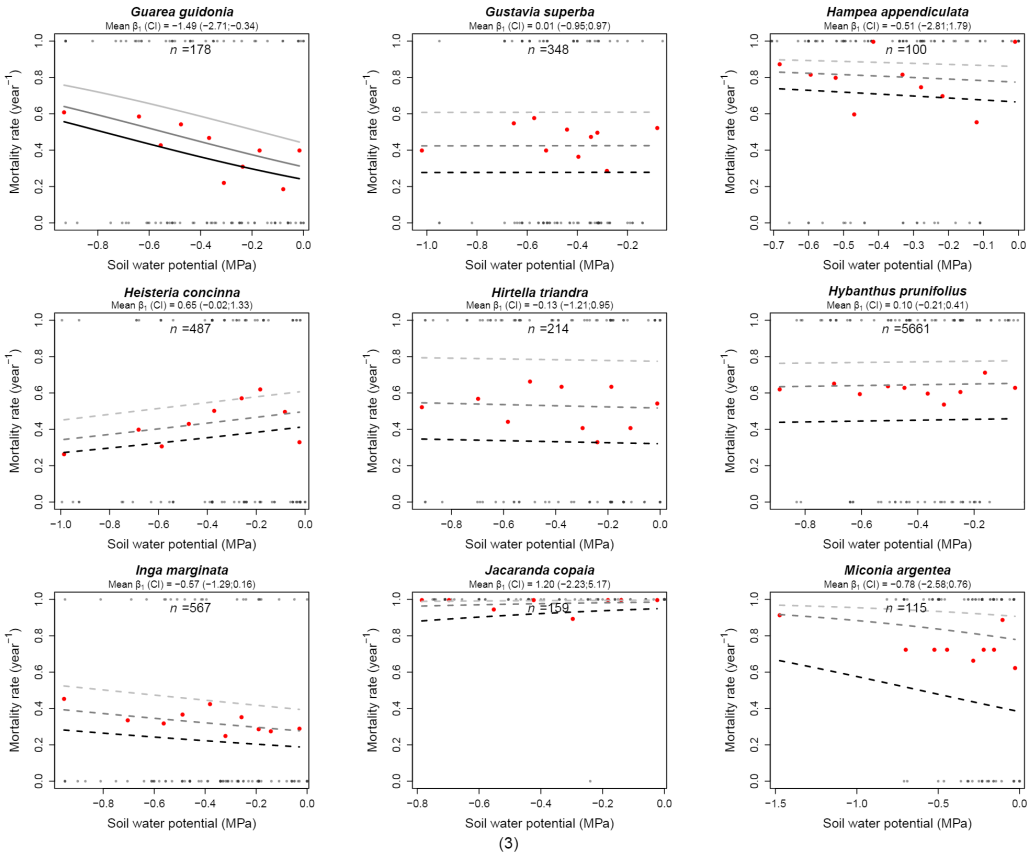
Figure S5 Responses of mortality rates to dry−season soil water potentials (page 1−6) and seedling height (page 7−11) for all species in the mortality model. Predicted responses (lines) and observed responses (dots) are shown. Mortality is predicted against soil water potential for three levels of seedling height (short, average, tall), and against seedling height for three moisture levels (dry, average and wet), with levels representing the 10th,50th and 90th percentile of the plotted species. The respective slopes of the response and their credible intervals are given above each panel. Red dots represent mean mortality for ten height or ten moisture classes, each containing 10% of the individuals of the species. Small grey dots show 100 randomly selected single observations.



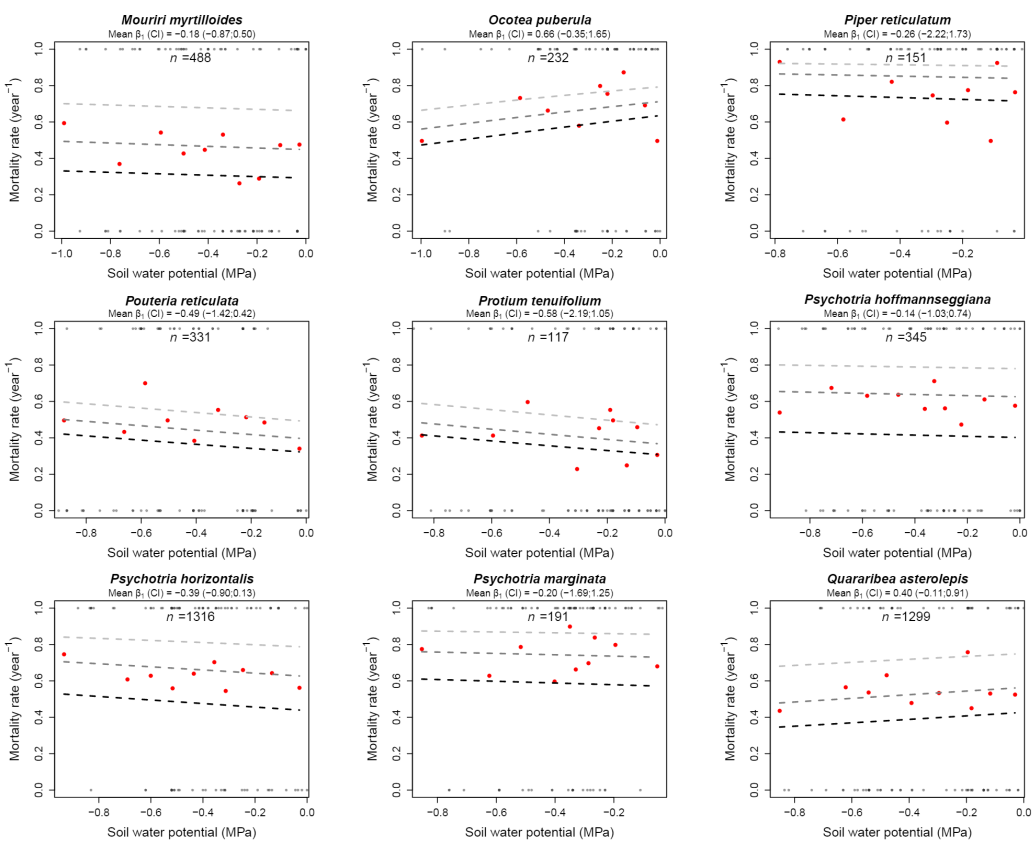
(1)



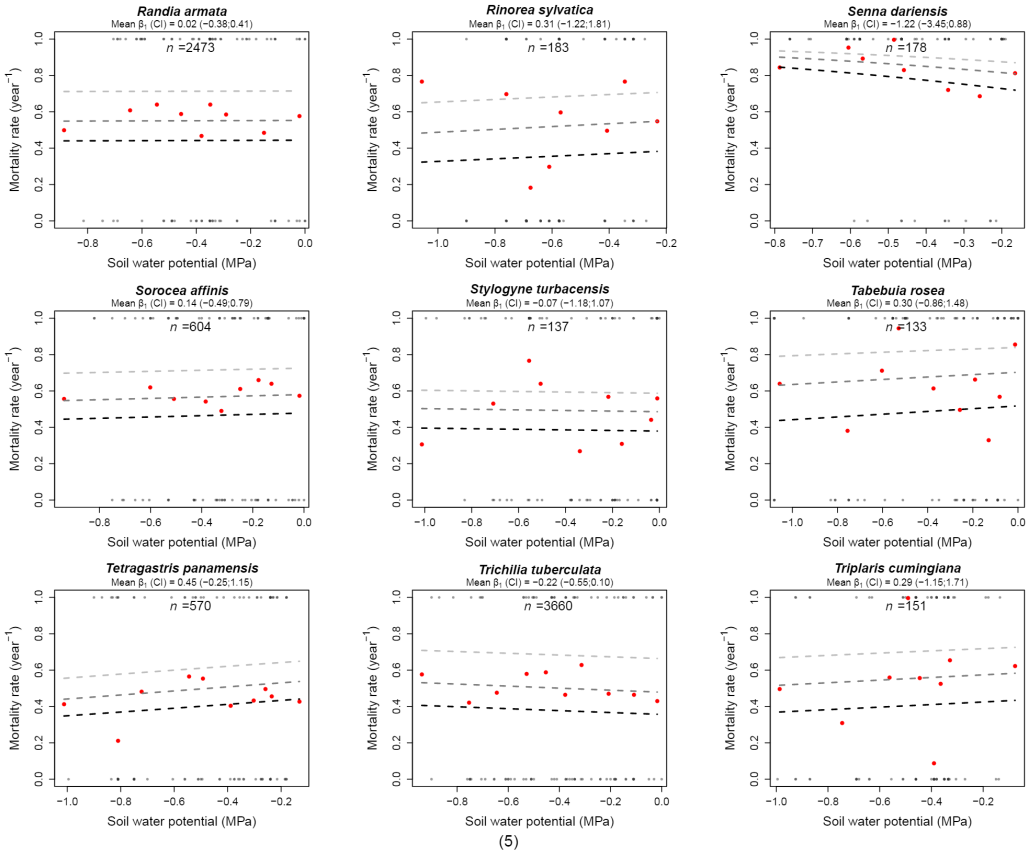
(2)


Guarea guidonia
Mean β1 (CI) = −1.49 (−2.71;−0.34)
n =178
Gustavia superba
Mean β1 (CI) = 0.01 (−0.95;0.97)
n =348
Hampea appendiculata
Mean β1 (CI) = −0.51 (−2.81;1.79)
n =100
Heisteria concinna
Mean β1 (CI) = 0.65 (−0.02;1.33)
n =487
Hirtella triandra
Mean β1 (CI) = −0.13 (−1.21;0.95)
n =214
Hybanthus prunifolius
Mean β1 (CI) = 0.10 (−0.21;0.41)
n =5661
Inga marginata
Mean β1 (CI) = −0.57 (−1.29;0.16)
n =567
Jacaranda copaia
Mean β1 (CI) = 1.20 (−2.23;5.17)
n =59
Miconia argentea
Mean β1 (CI) = −0.78 (−2.58;0.76)
n =115
Mortality rate (year−1)
Soil water potential (MPa)

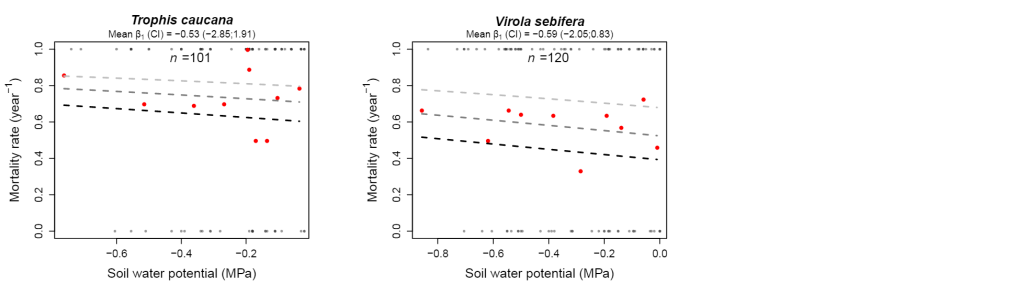
(3)


Mouriri myrtilloides
Mean β1 (CI) = −0.18 (−0.87;0.50)
n =488
Ocotea puberula
Mean β1 (CI) = 0.66 (−0.35;1.65)
n =232
Piper reticulatum
Mean β1 (CI) = −0.26 (−2.22;1.73)
n =151
Pouteria reticulata
Mean β1 (CI) = −0.49 (−1.42;0.42)
n =331
Protium tenuifolium
Mean β1 (CI) = −0.58 (−2.19;1.05)
n =117
Psychotria hoffmannseggiana
Mean β1 (CI) = −0.14 (−1.03;0.74)
n =345
Psychotria horizontalis
Mean β1 (CI) = −0.39 (−0.90;0.13)
n =1316
Psychotria marginata
Mean β1 (CI) = −0.20 (−1.69;1.25)
n =191
Quararibea asterolepis
Mean β1 (CI) = 0.40 (−0.11;0.91)
n =1299
Mortality rate (year−1)
Soil water potential (MPa)

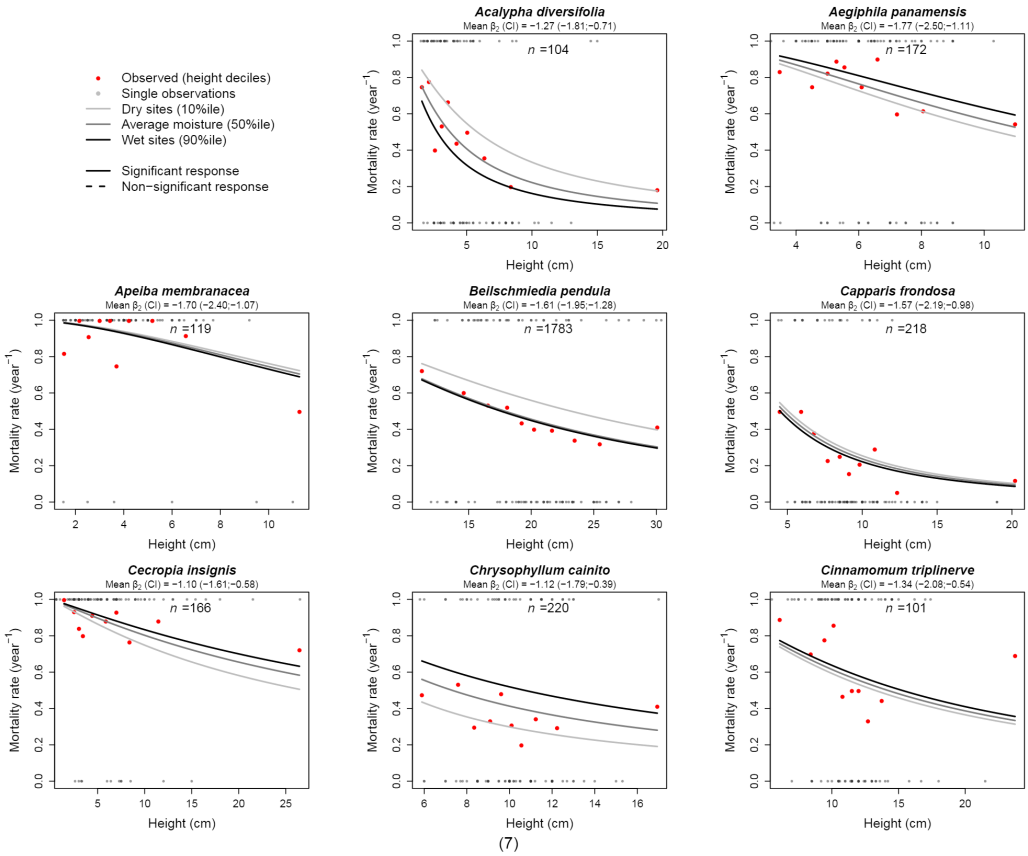
(4)


Randia armata
Mean β1 (CI) = 0.02 (−0.38;0.41)
n =2473
Rinorea sylvatica
Mean β1 (CI) = 0.31 (−1.22;1.81)
n =183
Senna dariensis
Mean β1 (CI) = −1.22 (−3.45;0.88)
n =178
Sorocea affinis
Mean β1 (CI) = 0.14 (−0.49;0.79)
n =604
Stylogyne turbacensis
Mean β1 (CI) = −0.07 (−1.18;1.07)
n =137
Tabebuia rosea
Mean β1 (CI) = 0.30 (−0.86;1.48)
n =133
Tetragastris panamensis
Mean β1 (CI) = 0.45 (−0.25;1.15)
n =570
Trichilia tuberculata
Mean β1 (CI) = −0.22 (−0.55;0.10)
n =3660
Triplaris cumingiana
Mean β1 (CI) = 0.29 (−1.15;1.71)
n =151
Mortality rate (year−1)
Soil water potential (MPa)

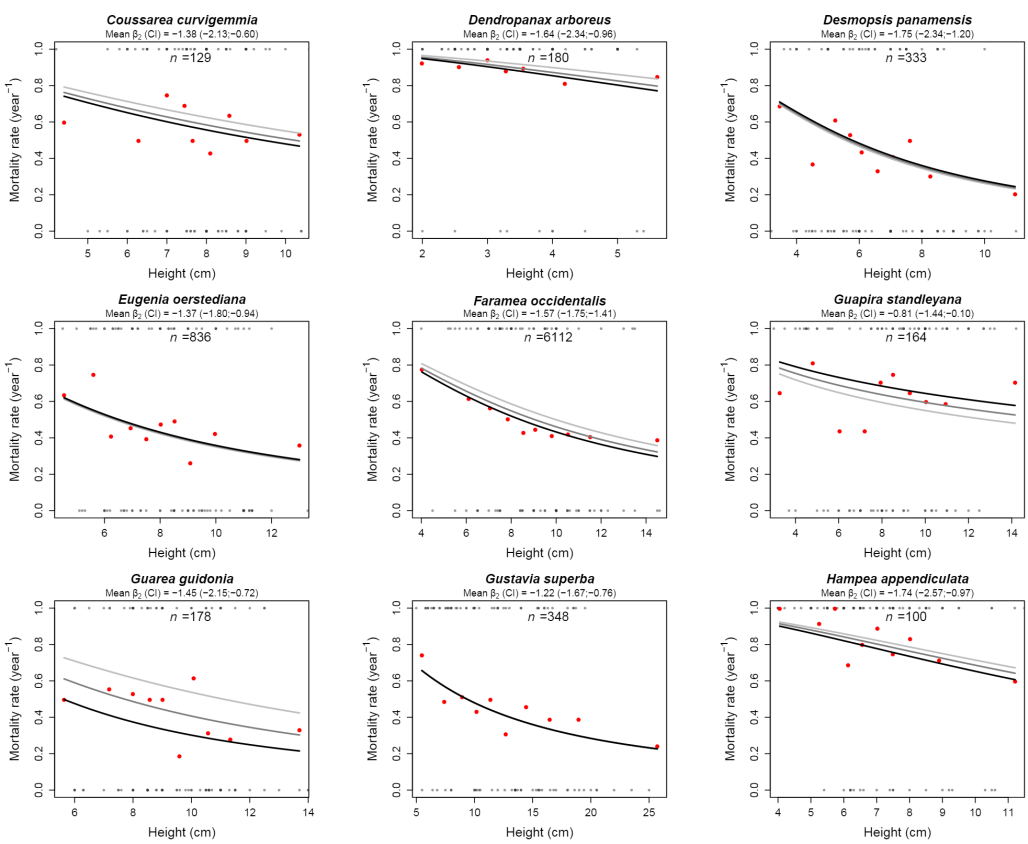
(5)


Trophis caucana
Mean β1 (CI) = −0.53 (−2.85;1.91)
n =101
Virola sebifera
Mean β1 (CI) = −0.59 (−2.05;0.83)
n =120
Mortality rate (year−1)
Soil water potential (MPa)

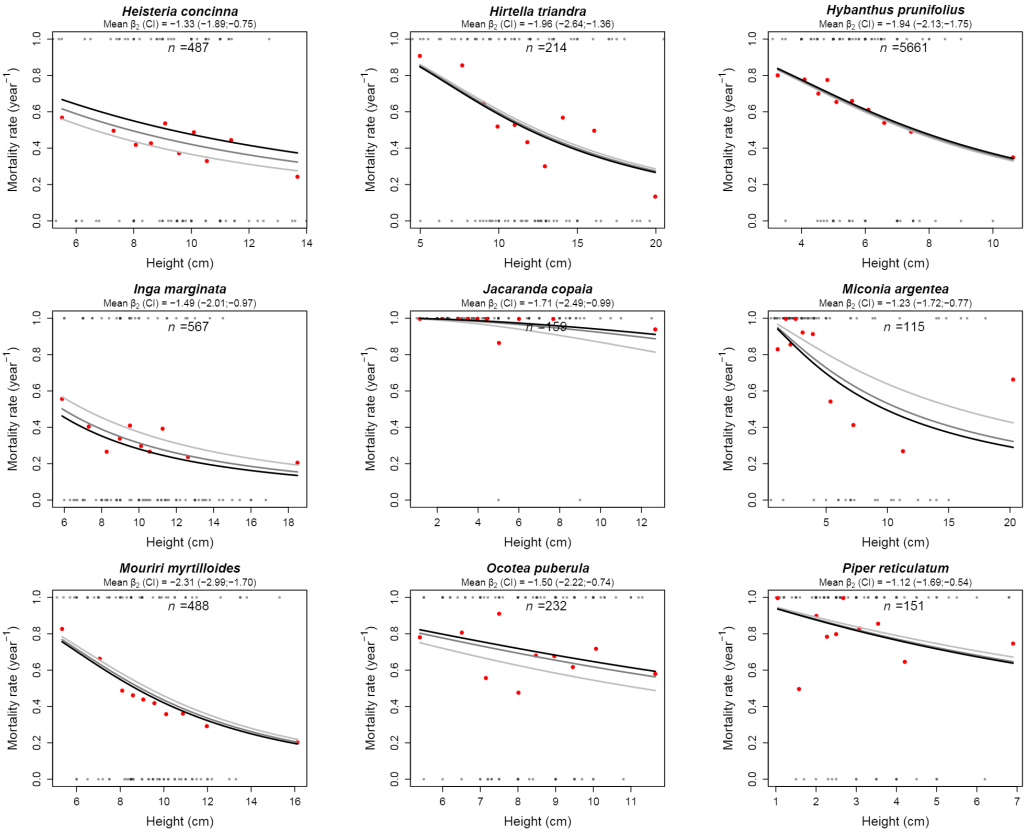
(6)


Observed (height deciles)
Single observations
Dry sites (10%ile)
Average moisture (50%ile)
Wet sites (90%ile)
Significant response
Non−significant response
Acalypha diversifolia
Mean β2 (CI) = −1.27 (−1.81;−0.71)
n =104
Aegiphila panamensis
Mean β2 (CI) = −1.77 (−2.50;−1.11)
n =172
Apeiba membranacea
Mean β2 (CI) = −1.70 (−2.40;−1.07)
n =119
Beilschmiedia pendula
Mean β2 (CI) = −1.61 (−1.95;−1.28)
n =1783
Capparis frondosa
Mean β2 (CI) = −1.57 (−2.19;−0.98)
n =218
Cecropia insignis
Mean β2 (CI) = −1.10 (−1.61;−0.58)
n =166
Chrysophyllum cainito
Mean β2 (CI) = −1.12 (−1.79;−0.39)
n =220
Cinnamomum triplinerve
Mean β2 (CI) = −1.34 (−2.08;−0.54)
n =101
Mortality rate (year−1)
Height (cm)

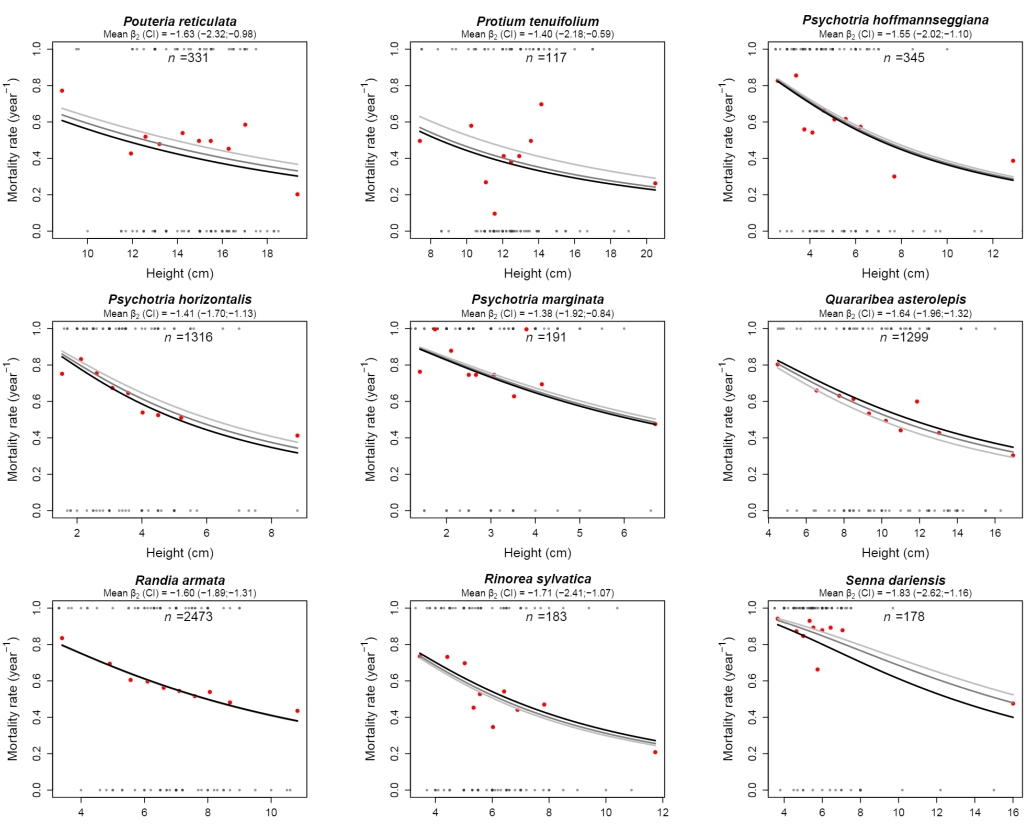
(7)


Coussarea curvigemmia
Mean β2 (CI) = −1.38 (−2.13;−0.60)
n =129
Dendropanax arboreus
Mean β2 (CI) = −1.64 (−2.34;−0.96)
n =180
Desmopsis panamensis
Mean β2 (CI) = −1.75 (−2.34;−1.20)
n =333
Eugenia oerstediana
Mean β2 (CI) = −1.37 (−1.80;−0.94)
n =836
Faramea occidentalis
Mean β2 (CI) = −1.57 (−1.75;−1.41)
n =6112
Guapira standleyana
Mean β2 (CI) = −0.81 (−1.44;−0.10)
n =164
Guarea guidonia
Mean β2 (CI) = −1.45 (−2.15;−0.72)
n =178
Gustavia superba
Mean β2 (CI) = −1.22 (−1.67;−0.76)
n =348
Hampea appendiculata
Mean β2 (CI) = −1.74 (−2.57;−0.97)
n =100
Mortality rate (year−1)
Height (cm)

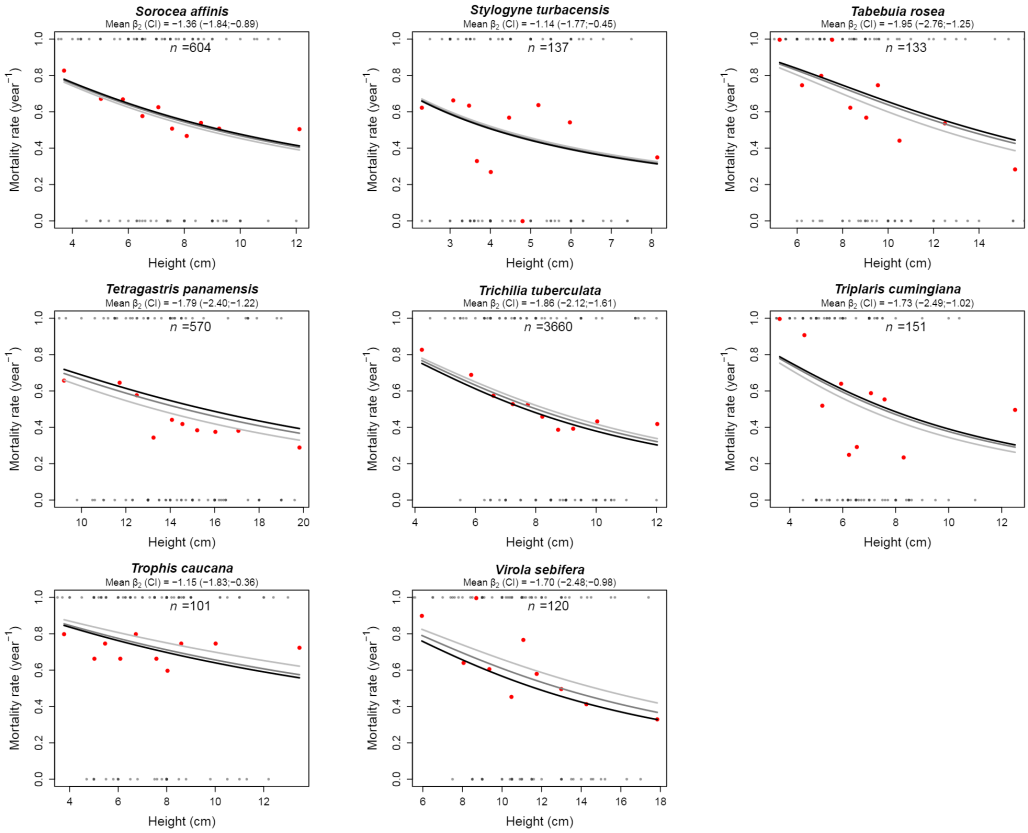
(8)


Heisteria concinna
Mean β2 (CI) = −1.33 (−1.89;−0.75)
n =487
Hirtella triandra
Mean β2 (CI) = −1.96 (−2.64;−1.36)
n =214
Hybanthus prunifolius
Mean β2 (CI) = −1.94 (−2.13;−1.75)
n =5661
Inga marginata
Mean β2 (CI) = −1.49 (−2.01;−0.97)
n =567
Jacaranda copaia
Mean β2 (CI) = −1.71 (−2.49;−0.99)
n =159
Miconia argentea
Mean β2 (CI) = −1.23 (−1.72;−0.77)
n =115
Mouriri myrtilloides
Mean β2 (CI) = −2.31 (−2.99;−1.70)
n =488
Ocotea puberula
Mean β2 (CI) = −1.50 (−2.22;−0.74)
n =232
Piper reticulatum
Mean β2 (CI) = −1.12 (−1.69;−0.54)
n =151
Mortality rate (year−1)
Height (cm)

(9)

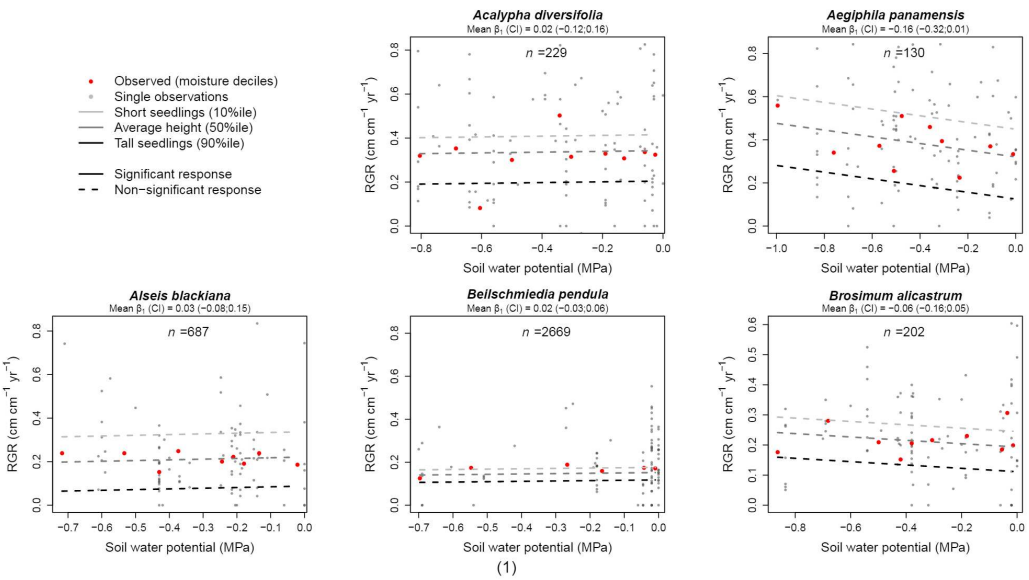

Pouteria reticulata
Mean β2 (CI) = −1.63 (−2.32;−0.98)
n =331
Protium tenuifolium
Mean β2 (CI) = −1.40 (−2.18;−0.59)
n =117
Psychotria hoffmannseggiana
Mean β2 (CI) = −1.55 (−2.02;−1.10)
n =345
Psychotria horizontalis
Mean β2 (CI) = −1.41 (−1.70;−1.13)
n =1316
Psychotria marginata
Mean β2 (CI) = −1.38 (−1.92;−0.84)
n =191
Quararibea asterolepis
Mean β2 (CI) = −1.64 (−1.96;−1.32)
n =1299
Randia armata
Mean β2 (CI) = −1.60 (−1.89;−1.31)
n =2473
Rinorea sylvatica
Mean β2 (CI) = −1.71 (−2.41;−1.07)
n =183
Senna dariensis
Mean β2 (CI) = −1.83 (−2.62;−1.16)
n =178
Mortality rate (year−1)
Height (cm)

(10)

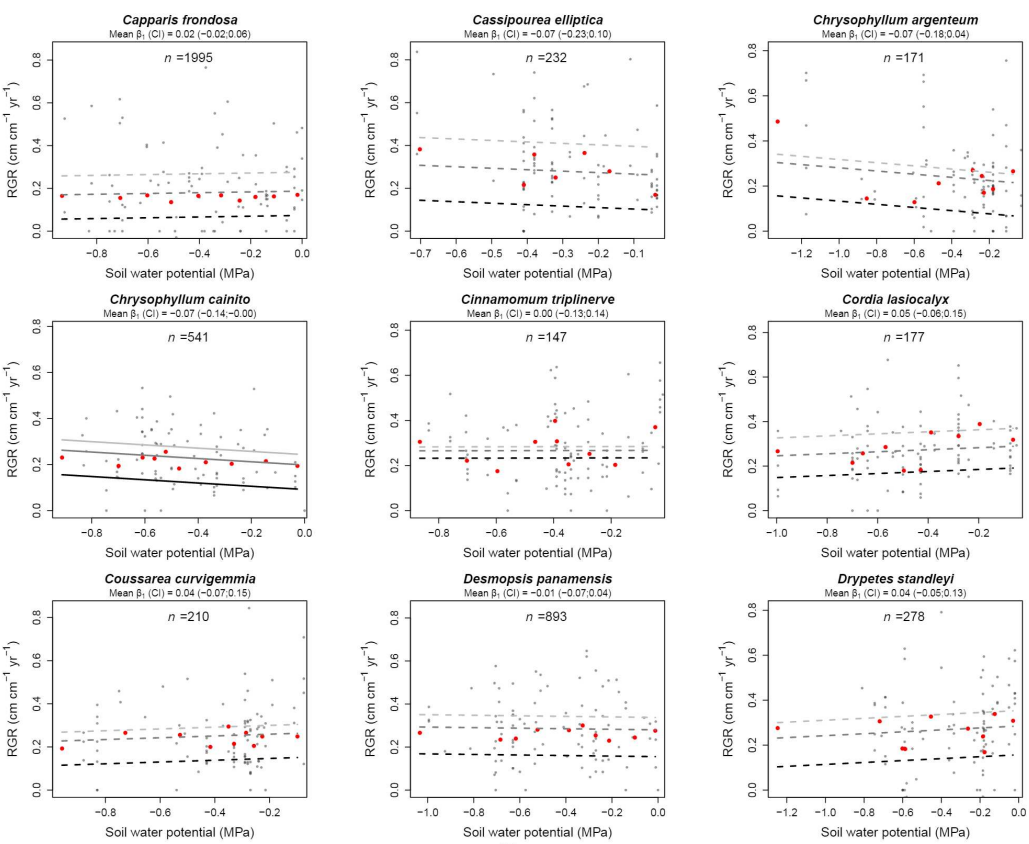

Sorocea affinis
Mean β2 (CI) = −1.36 (−1.84;−0.89)
n =604
Stylogyne turbacensis
Mean β2 (CI) = −1.14 (−1.77;−0.45)
n =137
Tabebuia rosea
Mean β2 (CI) = −1.95 (−2.76;−1.25)
n =133
Tetragastris panamensis
Mean β2 (CI) = −1.79 (−2.40;−1.22)
n =570
Trichilia tuberculata
Mean β2 (CI) = −1.86 (−2.12;−1.61)
n =3660
Triplaris cumingiana
Mean β2 (CI) = −1.73 (−2.49;−1.02)
n =151
Trophis caucana
Mean β2 (CI) = −1.15 (−1.83;−0.36)
n =101
Virola sebifera
Mean β2 (CI) = −1.70 (−2.48;−0.98)
n =120
Mortality rate (year−1)
Height (cm)

(11)

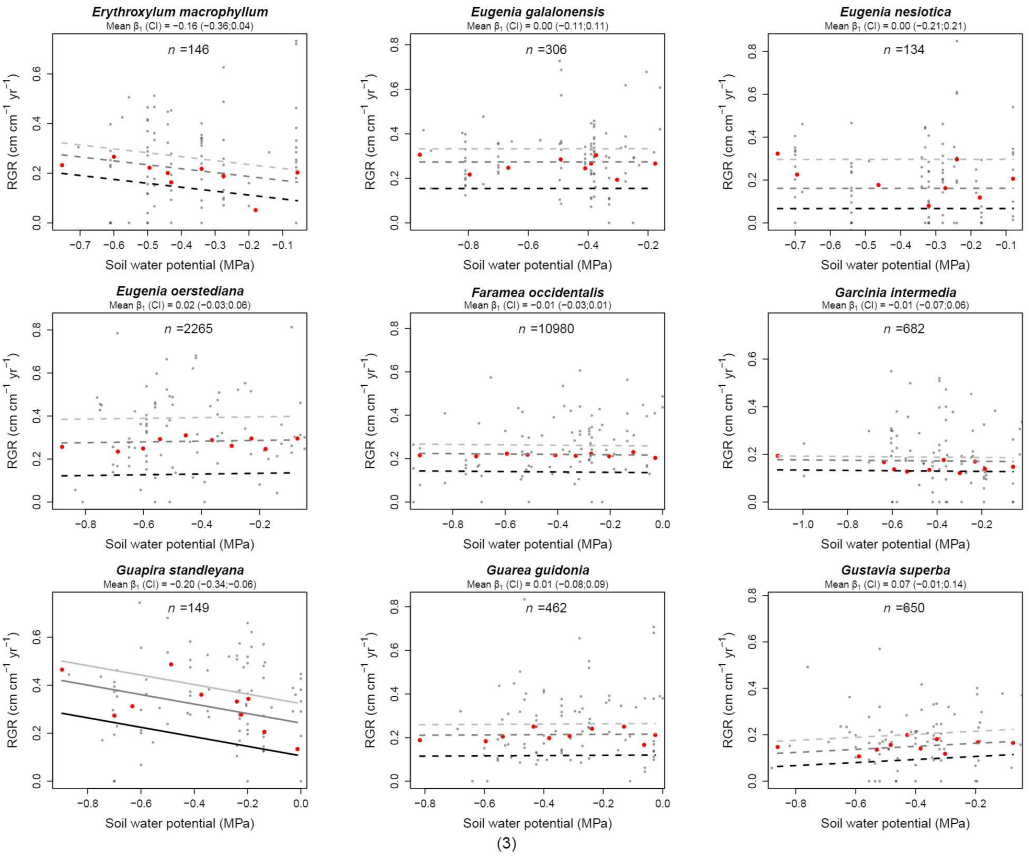
Figure S6 Responses of relative growth rates (RGR) to dry−season soil water potentials (page 1−7) and seedling height (page 8−13) for all species in the growth model with all growth observations (presented in Appendix S3). Predicted responses (lines) and observed responses (dots) are shown. Growth is predicted against soil water potential for three levels of seedling height (short, average, tall), and against seedling height for three moisture levels (dry, average and wet), with levels representing the 10th, 50th and 90th percentile of the plotted species. The respective slopes of the response and their credible intervals are given above each panel. Red dots represent mean RGR for ten height or ten moisture classes, each containing 10% of the individuals of the species. Small grey dots show 100 randomly selected single observations.



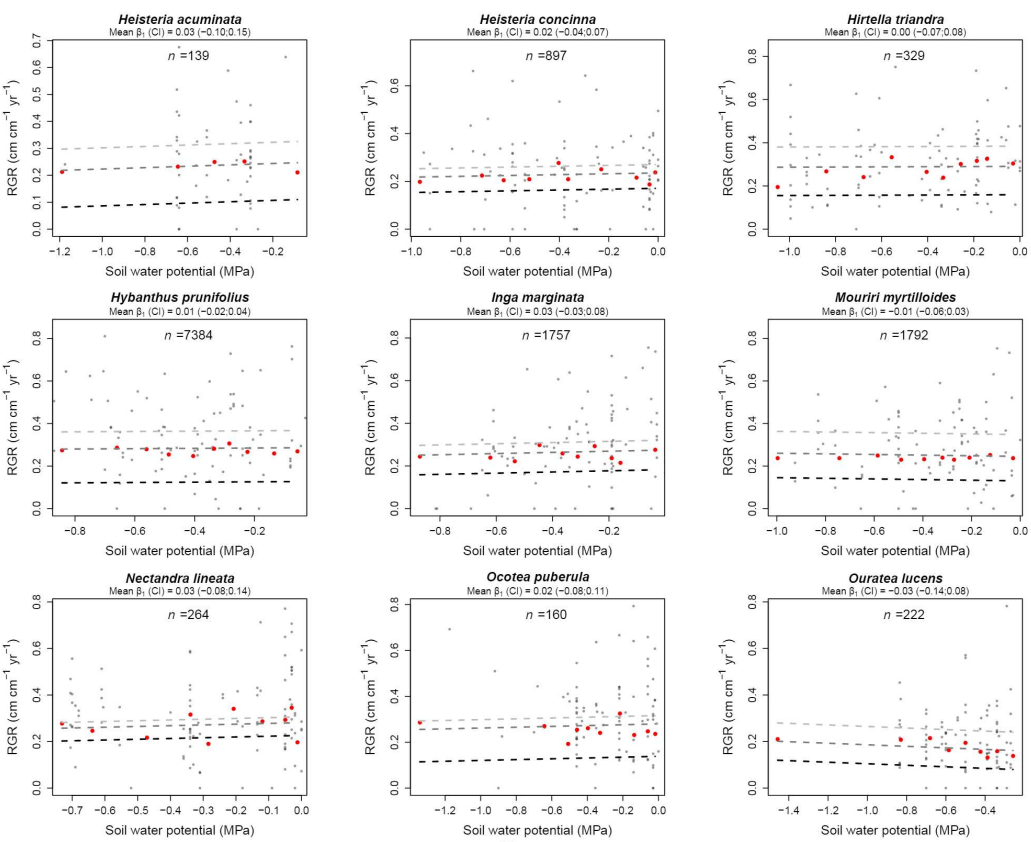
(1)



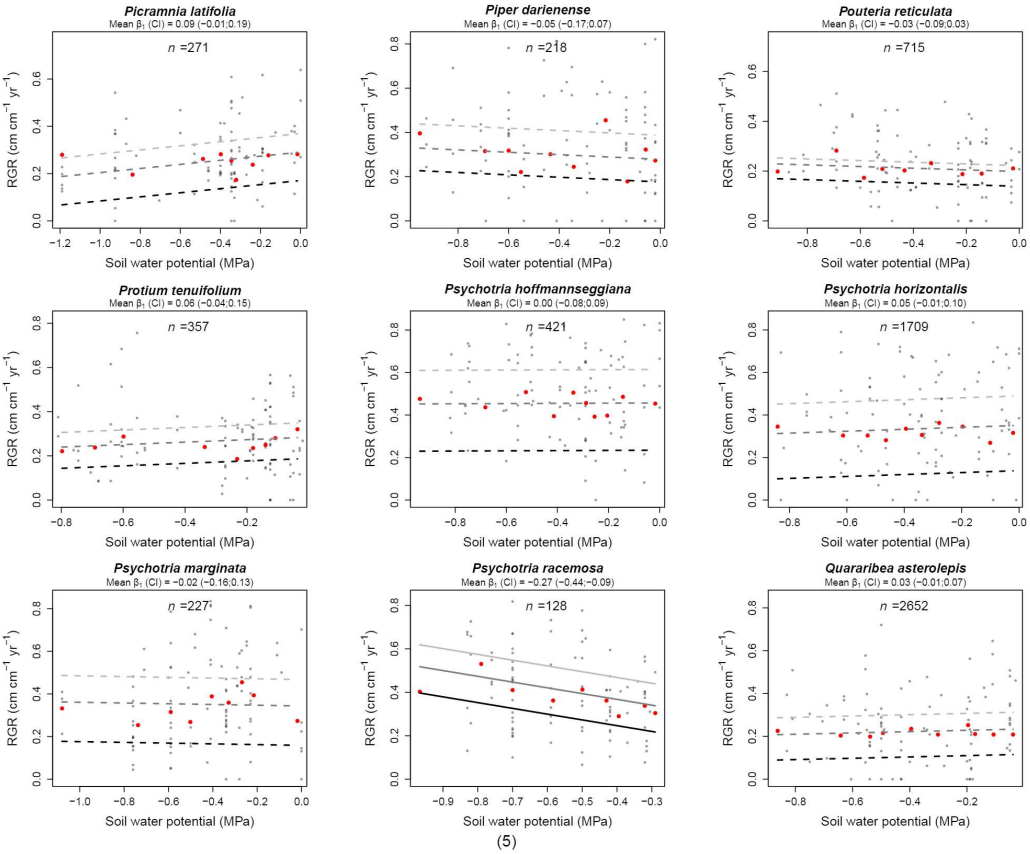
(2)


Erythroxylum macrophyllum
Mean β1 (CI) = −0.16 (−0.36;0.04)
n =146
Eugenia galalonensis
Mean β1 (CI) = 0.00 (−0.11;0.11)
n =306
Eugenia nesiotica
Mean β1 (CI) = 0.00 (−0.21;0.21)
n =134
Eugenia oerstediana
Mean β1 (CI) = 0.02 (−0.03;0.06)
n =2265
Faramea occidentalis
Mean β1 (CI) = −0.01 (−0.03;0.01)
n =10980
Garcinia intermedia
Mean β1 (CI) = −0.01 (−0.07;0.06)
n =682
Guapira standleyana
Mean β1 (CI) = −0.20 (−0.34;−0.06)
n =149
Guarea guidonia
Mean β1 (CI) = 0.01 (−0.08;0.09)
n =462
Gustavia superba
Mean β1 (CI) = 0.07 (−0.01;0.14)
n =650
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

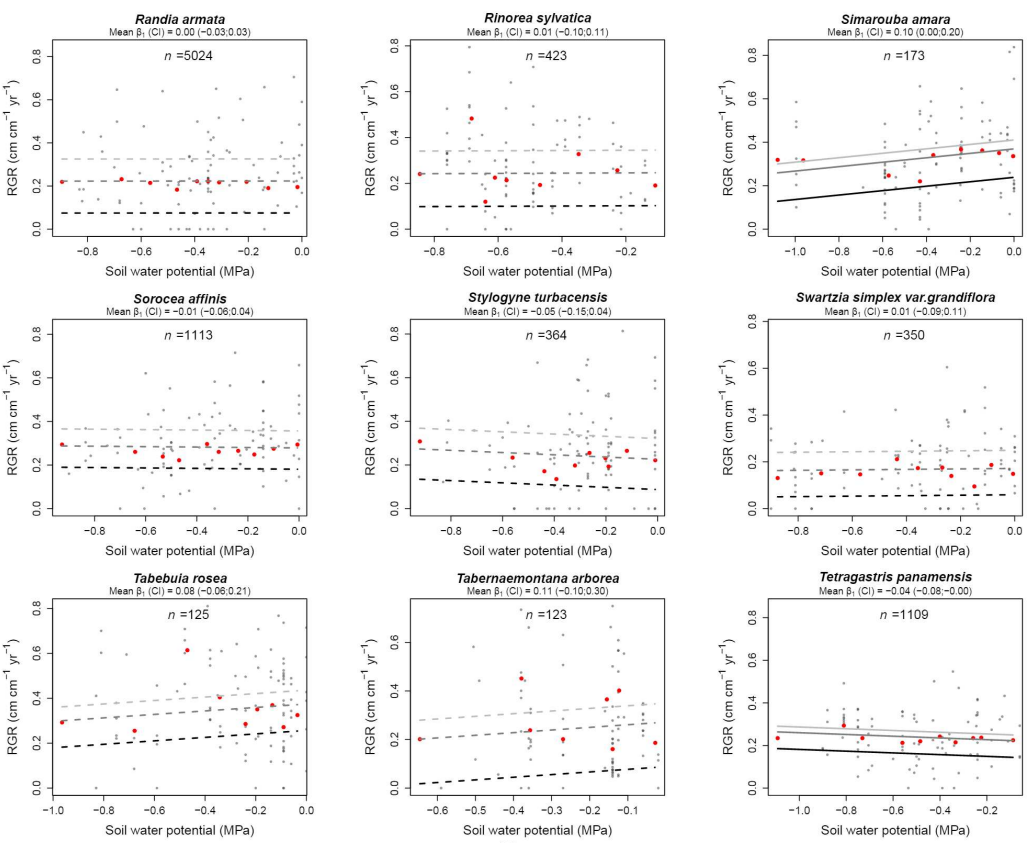
(3)


Heisteria acuminata
Mean β1 (CI) = 0.03 (−0.10;0.15)
n =139
Heisteria concinna
Mean β1 (CI) = 0.02 (−0.04;0.07)
n =897
Hirtella triandra
Mean β1 (CI) = 0.00 (−0.07;0.08)
n =329
Hybanthus prunifolius
Mean β1 (CI) = 0.01 (−0.02;0.04)
n =7384
Inga marginata
Mean β1 (CI) = 0.03 (−0.03;0.08)
n =1757
Mouriri myrtilloides
Mean β1 (CI) = −0.01 (−0.06;0.03)
n =1792
Nectandra lineata
Mean β1 (CI) = 0.03 (−0.08;0.14)
n =264
Ocotea puberula
Mean β1 (CI) = 0.02 (−0.08;0.11)
n =160
Ouratea lucens
Mean β1 (CI) = −0.03 (−0.14;0.08)
n =222
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

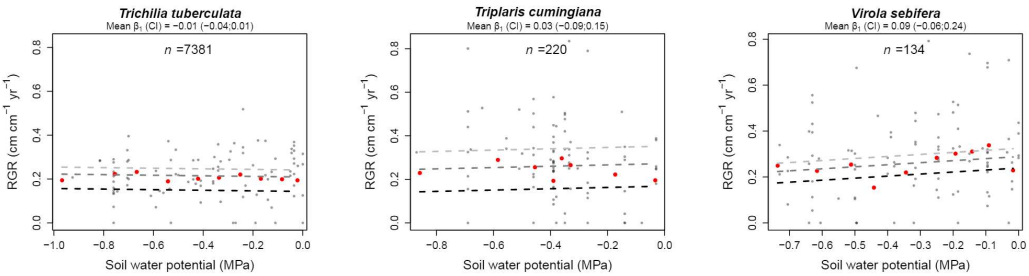
(4)


Picramnia latifolia
Mean β1 (CI) = 0.09 (−0.01;0.19)
n =271
Piper darienense
Mean β1 (CI) = −0.05 (−0.17;0.07)
n =218
Pouteria reticulata
Mean β1 (CI) = −0.03 (−0.09;0.03)
n =715
Protium tenuifolium
Mean β1 (CI) = 0.06 (−0.04;0.15)
n =357
Psychotria hoffmannseggiana
Mean β1 (CI) = 0.00 (−0.08;0.09)
n =421
Psychotria horizontalis
Mean β1 (CI) = 0.05 (−0.01;0.10)
n =1709
Psychotria marginata
Mean β1 (CI) = −0.02 (−0.16;0.13)
n =227
Psychotria racemosa
Mean β1 (CI) = −0.27 (−0.44;−0.09)
n =128
Quararibea asterolepis
Mean β1 (CI) = 0.03 (−0.01;0.07)
n =2652
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

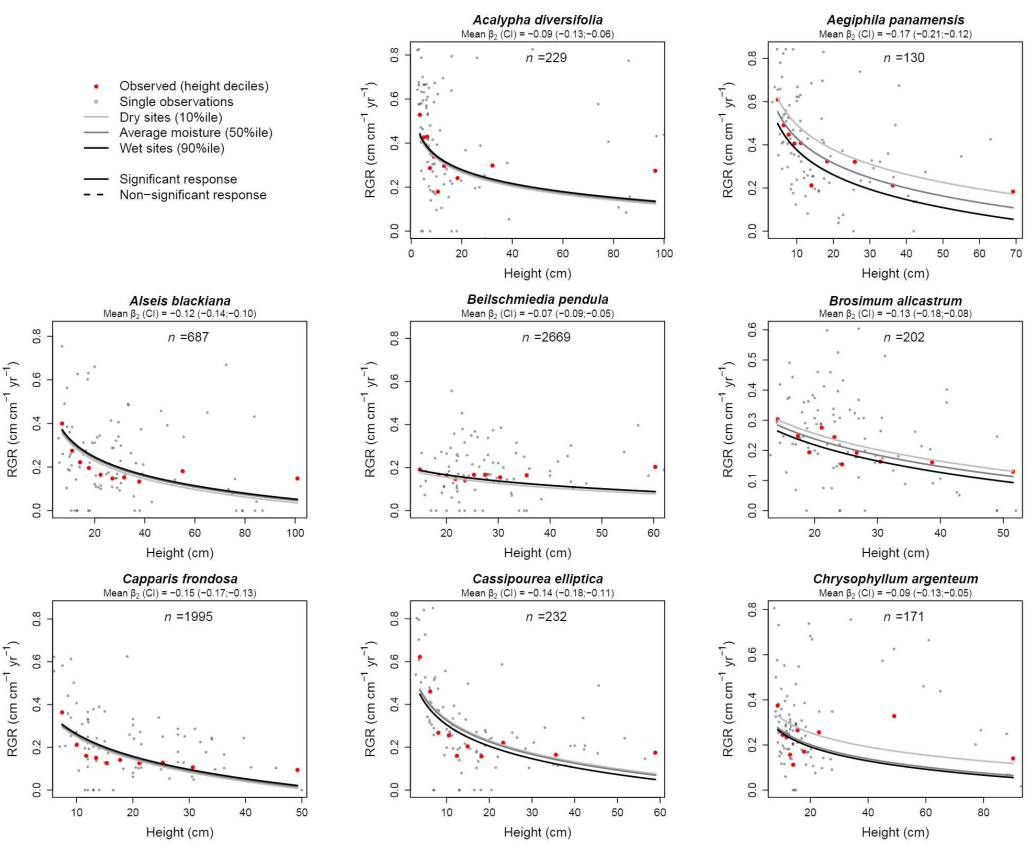
(5)


Randia armata
Mean β1 (CI) = 0.00 (−0.03;0.03)
n =5024
Rinorea sylvatica
Mean β1 (CI) = 0.01 (−0.10;0.11)
n =423
Simarouba amara
Mean β1 (CI) = 0.10 (0.00;0.20)
n =173
Sorocea affinis
Mean β1 (CI) = −0.01 (−0.06;0.04)
n =1113
Stylogyne turbacensis
Mean β1 (CI) = −0.05 (−0.15;0.04)
n =364
Swartzia simplex var.grandiflora
Mean β1 (CI) = 0.01 (−0.09;0.11)
n =350
Tabebuia rosea
Mean β1 (CI) = 0.08 (−0.06;0.21)
n =125
Tabernaemontana arborea
Mean β1 (CI) = 0.11 (−0.10;0.30)
n =123
Tetragastris panamensis
Mean β1 (CI) = −0.04 (−0.08;−0.00)
n =1109
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

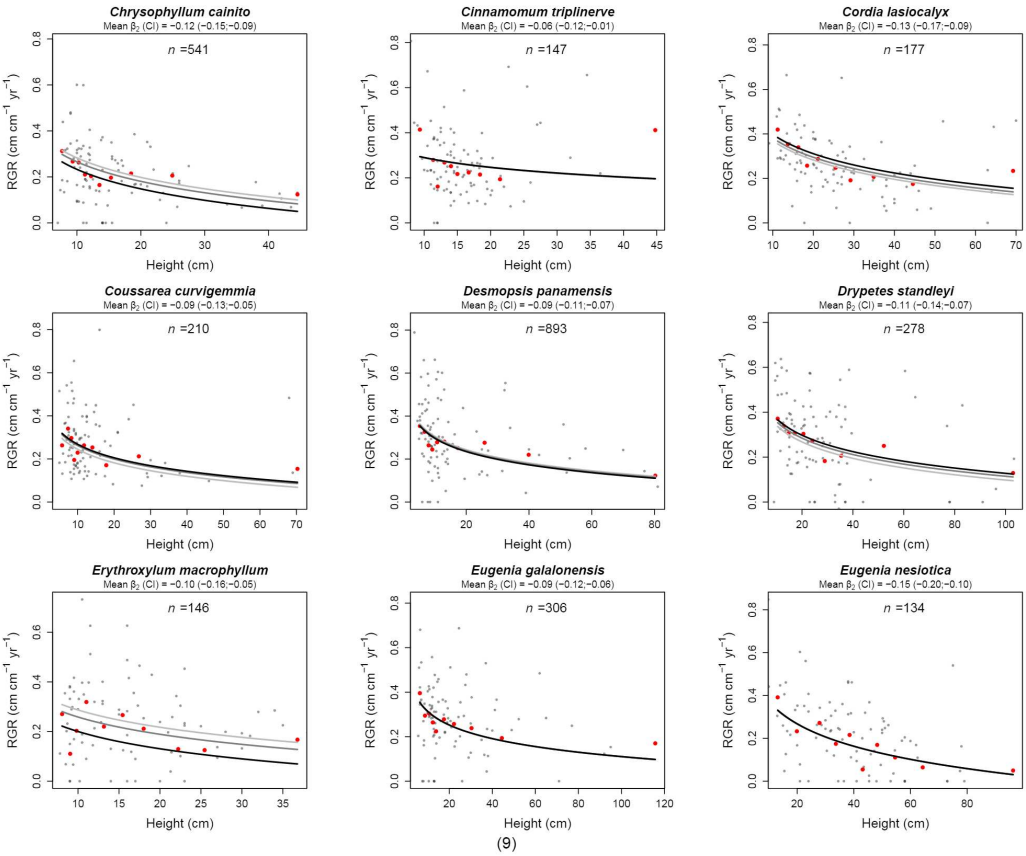
(6)


Trichilia tuberculata
Mean β1 (CI) = −0.01 (−0.04;0.01)
n =7381
Triplaris cumingiana
Mean β1 (CI) = 0.03 (−0.09;0.15)
n =220
Virola sebifera
Mean β1 (CI) = 0.09 (−0.06;0.24)
n =134
RGR (cm cm−1 yr−1)
Soil water potential (MPa)

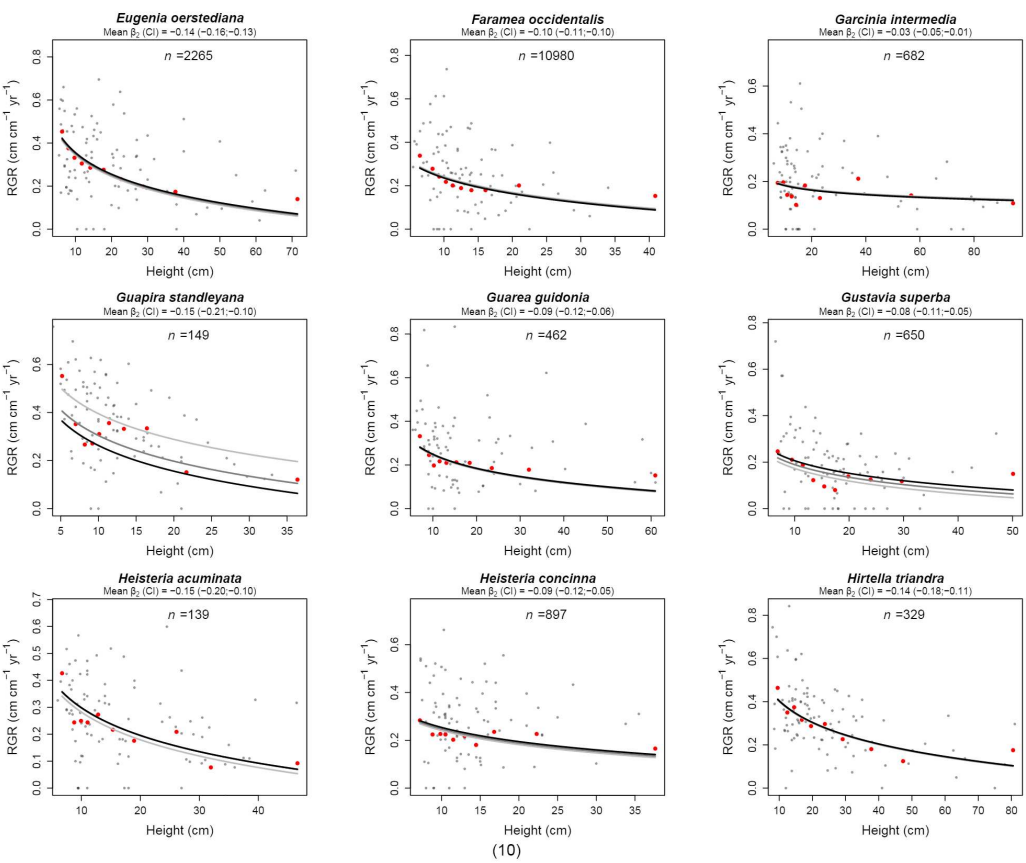
(7)


Observed (height deciles)
Single observations
Dry sites (10%ile)
Average moisture (50%ile)
Wet sites (90%ile)
Significant response
Non−significant response
Acalypha diversifolia
Mean β2 (CI) = −0.09 (−0.13;−0.06)
n =229
Aegiphila panamensis
Mean β2 (CI) = −0.17 (−0.21;−0.12)
n =130
Alseis blackiana
Mean β2 (CI) = −0.12 (−0.14;−0.10)
n =687
Beilschmiedia pendula
Mean β2 (CI) = −0.07 (−0.09;−0.05)
n =2669
Brosimum alicastrum
Mean β2 (CI) = −0.13 (−0.18;−0.08)
n =202
Capparis frondosa
Mean β2 (CI) = −0.15 (−0.17;−0.13)
n =1995
Cassipourea elliptica
Mean β2 (CI) = −0.14 (−0.18;−0.11)
n =232
Chrysophyllum argenteum
Mean β2 (CI) = −0.09 (−0.13;−0.05)
n =171
RGR (cm cm−1 yr−1)
Height (cm)

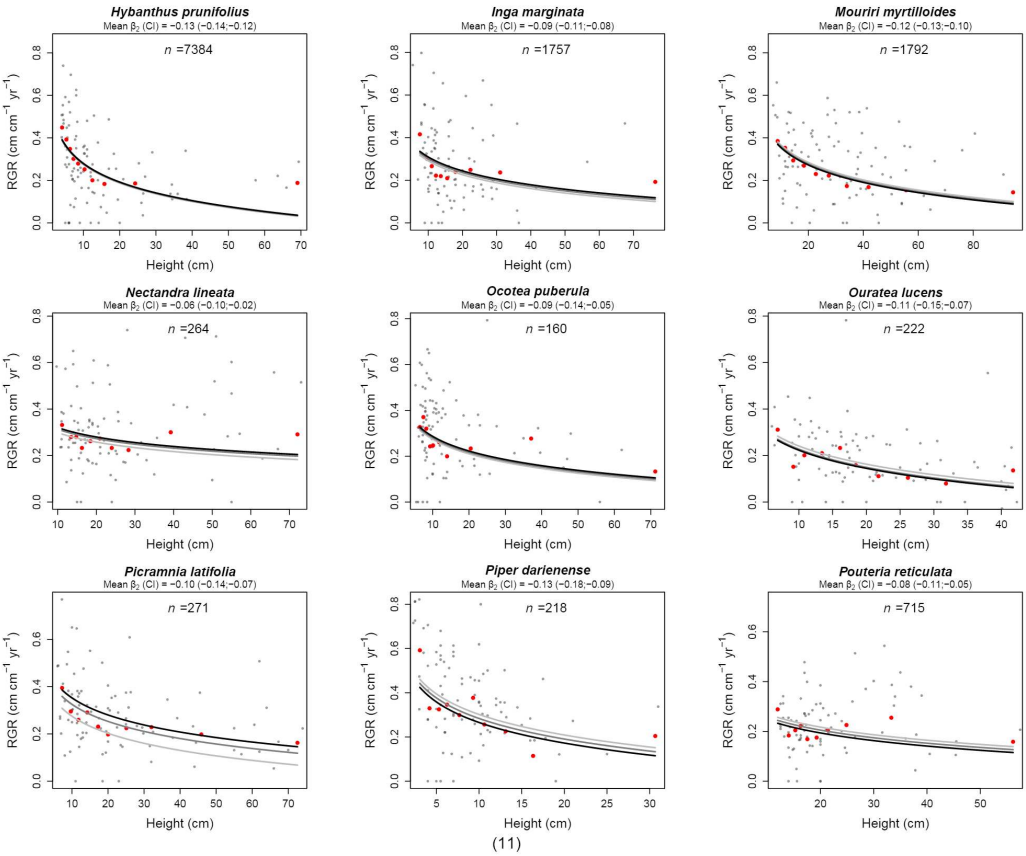
(8)


Chrysophyllum cainito
Mean β2 (CI) = −0.12 (−0.15;−0.09)
n =541
Cinnamomum triplinerve
Mean β2 (CI) = −0.06 (−0.12;−0.01)
n =147
Cordia lasiocalyx
Mean β2 (CI) = −0.13 (−0.17;−0.09)
n =177
Coussarea curvigemmia
Mean β2 (CI) = −0.09 (−0.13;−0.05)
n =210
Desmopsis panamensis
Mean β2 (CI) = −0.09 (−0.11;−0.07)
n =893
Drypetes standleyi
Mean β2 (CI) = −0.11 (−0.14;−0.07)
n =278
Erythroxylum macrophyllum
Mean β2 (CI) = −0.10 (−0.16;−0.05)
n =146
Eugenia galalonensis
Mean β2 (CI) = −0.09 (−0.12;−0.06)
n =306
Eugenia nesiotica
Mean β2 (CI) = −0.15 (−0.20;−0.10)
n =134
RGR (cm cm−1 yr−1)
Height (cm)

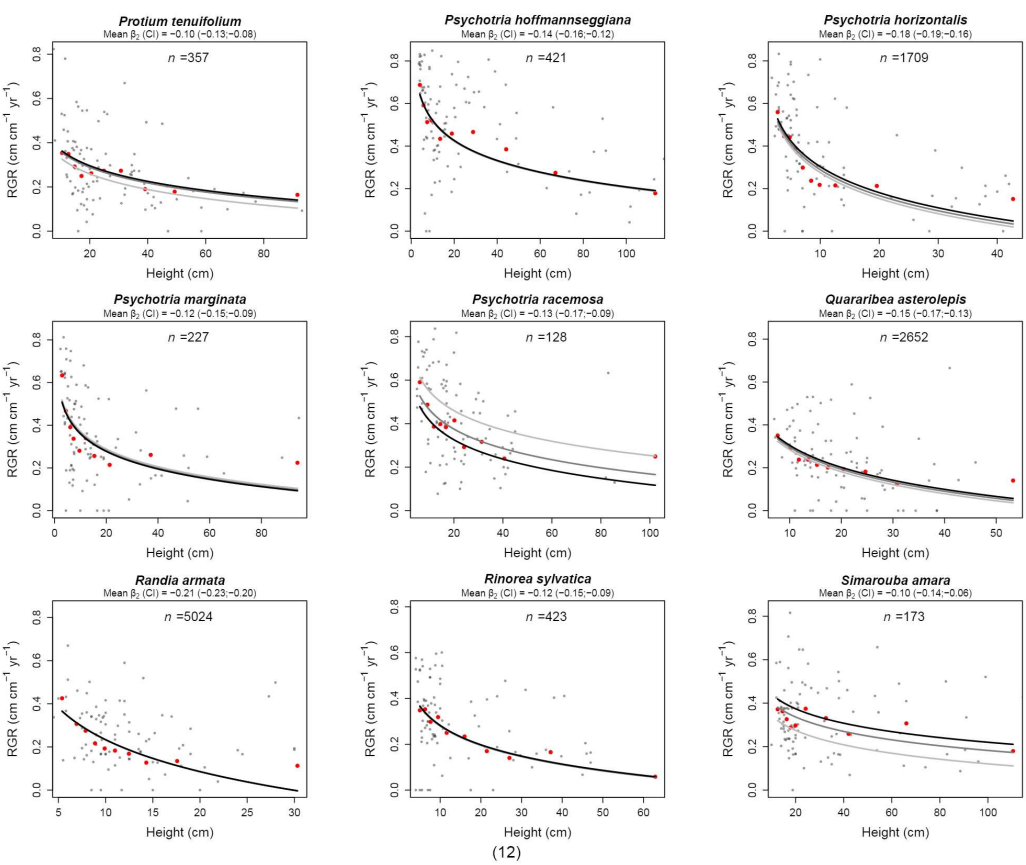
(9)


Eugenia oerstediana
Mean β2 (CI) = −0.14 (−0.16;−0.13)
n =2265
Faramea occidentalis
Mean β2 (CI) = −0.10 (−0.11;−0.10)
n =10980
Garcinia intermedia
Mean β2 (CI) = −0.03 (−0.05;−0.01)
n =682
Guapira standleyana
Mean β2 (CI) = −0.15 (−0.21;−0.10)
n =149
Guarea guidonia
Mean β2 (CI) = −0.09 (−0.12;−0.06)
n =462
Gustavia superba
Mean β2 (CI) = −0.08 (−0.11;−0.05)
n =650
Heisteria acuminata
Mean β2 (CI) = −0.15 (−0.20;−0.10)
n =139
Heisteria concinna
Mean β2 (CI) = −0.09 (−0.12;−0.05)
n =897
Hirtella triandra
Mean β2 (CI) = −0.14 (−0.18;−0.11)
n =329
RGR (cm cm−1 yr−1)
Height (cm)

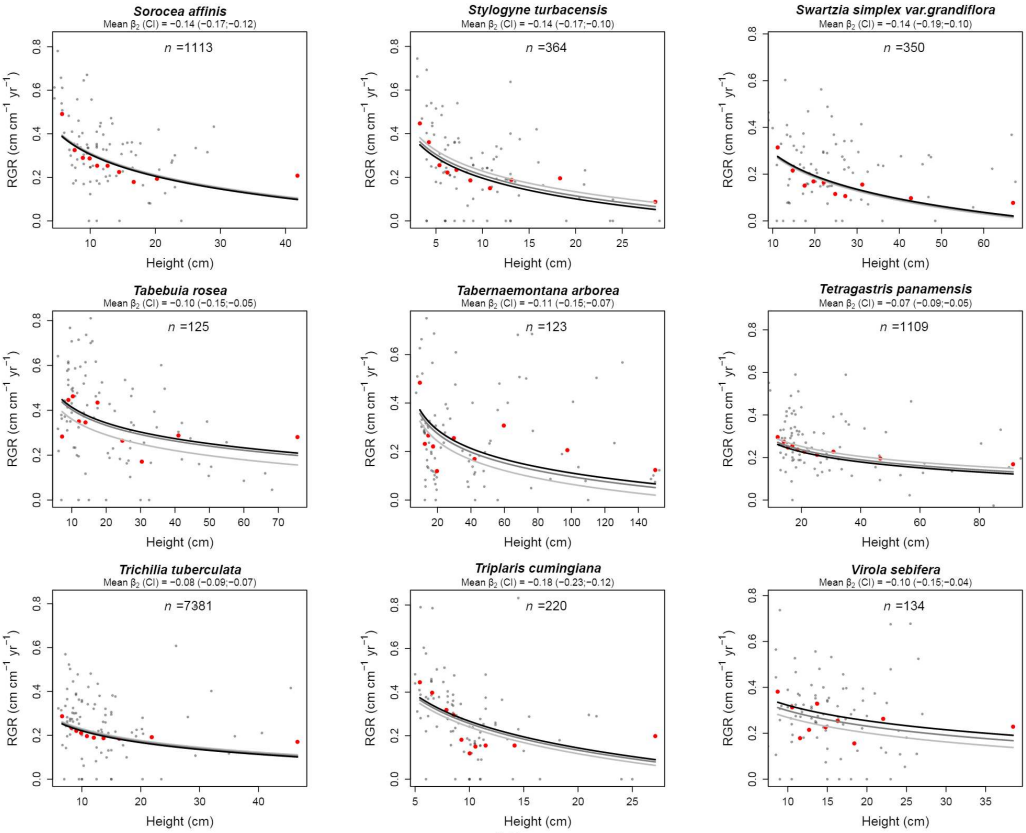
(10)


Hybanthus prunifolius
Mean β2 (CI) = −0.13 (−0.14;−0.12)
n =7384
Inga marginata
Mean β2 (CI) = −0.09 (−0.11;−0.08)
n =1757
Mouriri myrtilloides
Mean β2 (CI) = −0.12 (−0.13;−0.10)
n =1792
Nectandra lineata
Mean β2 (CI) = −0.06 (−0.10;−0.02)
n =264
Ocotea puberula
Mean β2 (CI) = −0.09 (−0.14;−0.05)
n =160
Ouratea lucens
Mean β2 (CI) = −0.11 (−0.15;−0.07)
n =222
Picramnia latifolia
Mean β2 (CI) = −0.10 (−0.14;−0.07)
n =271
Piper dilatatum
Mean β2 (CI) = −0.13 (−0.18;−0.09)
n =218
Pouteria reticulata
Mean β2 (CI) = −0.08 (−0.11;−0.05)
n =715
RGR (cm cm−1 yr−1)
Height (cm)

(11)


Protium tenuifolium
Mean β2 (CI) = −0.10 (−0.13;−0.08)
n =357
Psychotria hoffmannseggiana
Mean β2 (CI) = −0.14 (−0.16;−0.12)
n =421
Psychotria horizontalis
Mean β2 (CI) = −0.18 (−0.19;−0.16)
n =1709
Psychotria marginata
Mean β2 (CI) = −0.12 (−0.15;−0.09)
n =227
Psychotria racemosa
Mean β2 (CI) = −0.13 (−0.17;−0.09)
n =128
Quararibea asterolepis
Mean β2 (CI) = −0.15 (−0.17;−0.13)
n =2652
Randia armata
Mean β2 (CI) = −0.21 (−0.23;−0.20)
n =5024
Rinorea sylvatica
Mean β2 (CI) = −0.12 (−0.15;−0.09)
n =423
Simarouba amara
Mean β2 (CI) = −0.10 (−0.14;−0.06)
n =173
RGR (cm cm−1 yr−1)
Height (cm)

(12)


Sorocea affinis
Mean β2 (CI) = −0.14 (−0.17;−0.12)
n =1113
Stylogyne turbacensis
Mean β2 (CI) = −0.14 (−0.17;−0.10)
n =364
Swartzia simplex var.grandiflora
Mean β2 (CI) = −0.14 (−0.19;−0.10)
n =350
Tabebuia rosea
Mean β2 (CI) = −0.10 (−0.15;−0.05)
n =125
Tabernaemontana arborea
Mean β2 (CI) = −0.11 (−0.15;−0.07)
n =123
Tetragastris panamensis
Mean β2 (CI) = −0.07 (−0.09;−0.05)
n =1109
Trichilia tuberculata
Mean β2 (CI) = −0.08 (−0.09;−0.07)
n =7381
Triplaris cumingiana
Mean β2 (CI) = −0.18 (−0.23;−0.12)
n =220
Virola sebifera
Mean β2 (CI) = −0.10 (−0.15;−0.04)
n =134
RGR (cm cm−1 yr−1)
Height (cm)

(13)

Performance of tropical forest seedlings facing shade and drought: an interspecific trade-off in demographic responses

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[5] Department of Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, 95447 Bayreuth, Germany

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SUPPLEMENTARY INFORMATION

Contents

1. Supplementary figures and tables

Tables S1-S2 and Figure S1 present the responses of all 91 species in the study to shade and drought, and are included in this file from page 19 onwards.

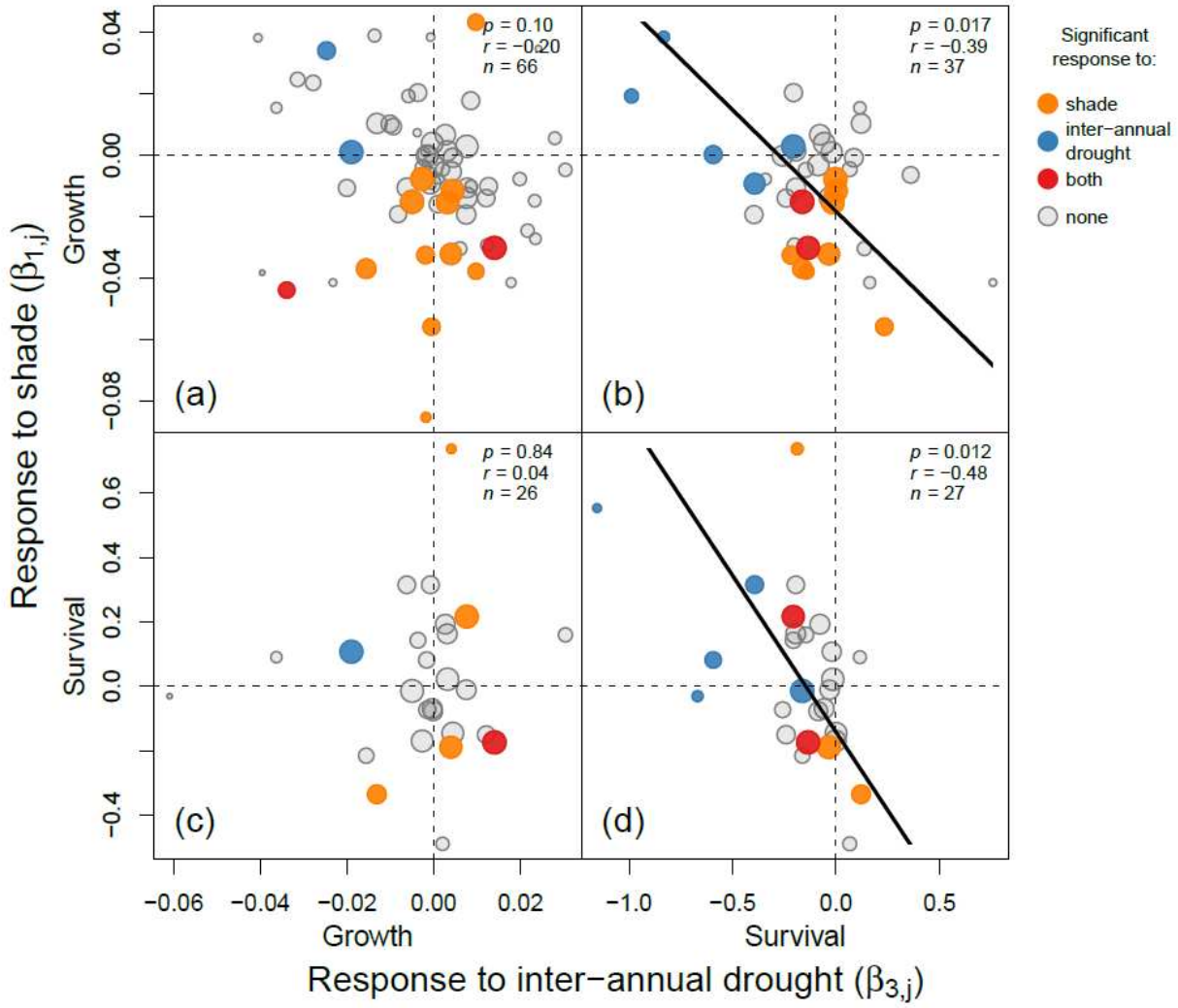


Figure S1.1 Relationships between species responses to shade and inter-annual drought (i.e. dry season severity) for growth (a), survival (d), or growth versus survival (b,c) when individuals that resprouted, were visually damaged or infected by pathogens were included in the analysis. Solid lines indicate significant relationships ($p < 0.05$). Negative relationships indicate a trade-off between shade and drought responses. Correlations are weighted by the uncertainty in species tolerances (smaller dots have higher uncertainty and lower weight, see equation (5) in the main text). Colours identify species with insignificant (grey) or significant responses to shade (orange), inter-annual drought (blue) or both (red).

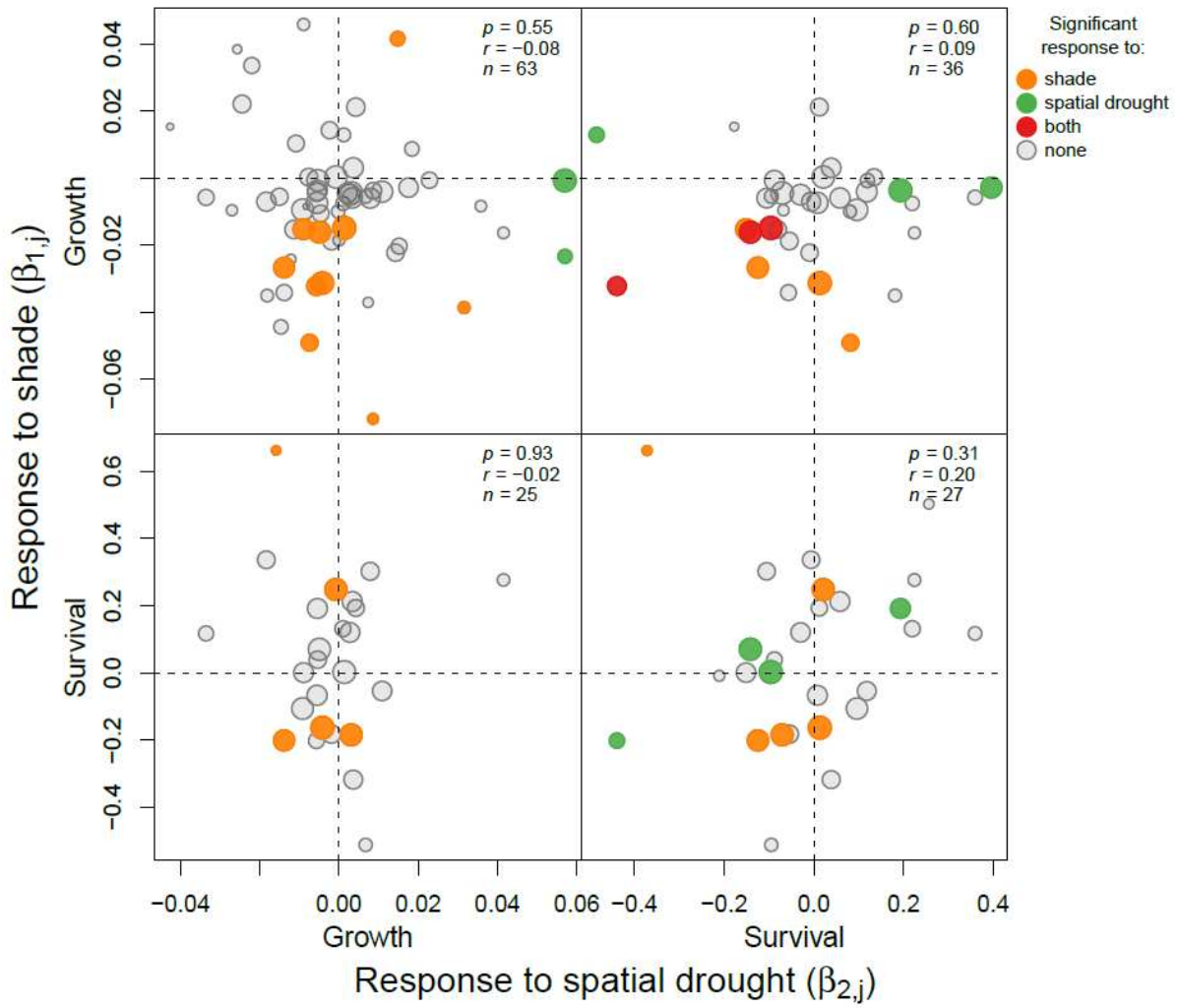


Figure S1.2 Relationships between species responses to shade and spatial drought (i.e. the inverse of soil water potential) for growth (a), survival (d), or growth versus survival (b,c). None of the relationships was significant. Correlations are weighted by the uncertainty in species tolerances (smaller dots have higher uncertainty and lower weight, see equation (5) in the main text). Colours identify species with insignificant (grey) or significant responses to shade (orange), spatial drought (green) or both (red).

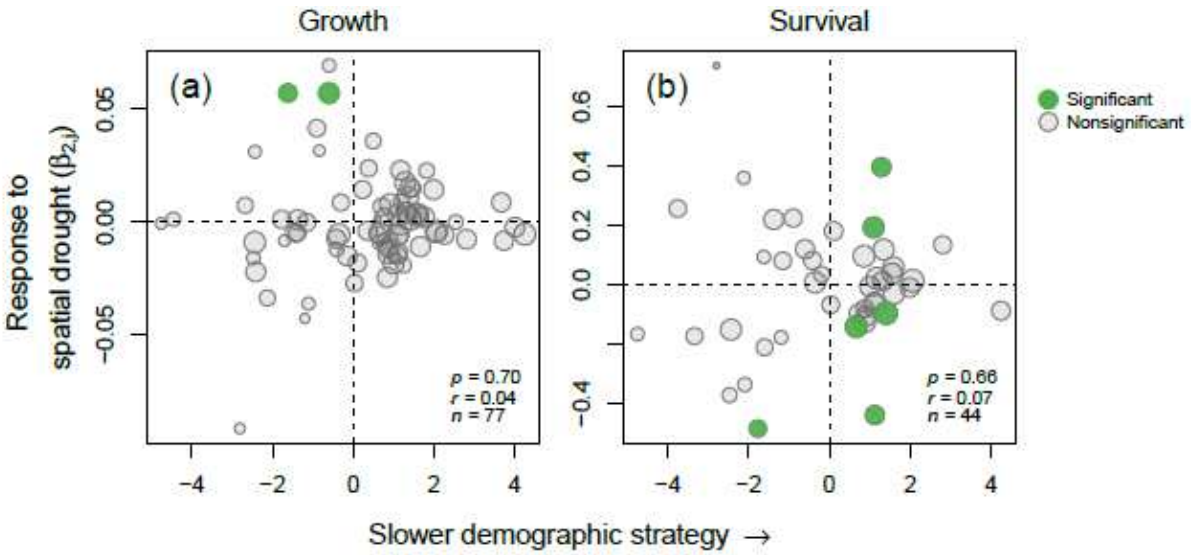


Figure S1.3 Relationships between the fast-slow continuum and responses to spatial drought for (a) growth and (b) survival. The position of species along the continuum was quantified based on a weighted PCA of demographic rates (growth, survival, number of sapling recruits) of trees ≥ 1 cm dbh recorded in the BCI 50-ha plot[1]. Low and high scores correspond to species with fast and slow demographic strategies, respectively. Colours identify species with insignificant (grey) or significant responses to shade (orange) or spatial drought (green). Relationships were consistent when the fast-slow continuum was calculated using seedling performance and/or seed number additionally (see Table S1.2).

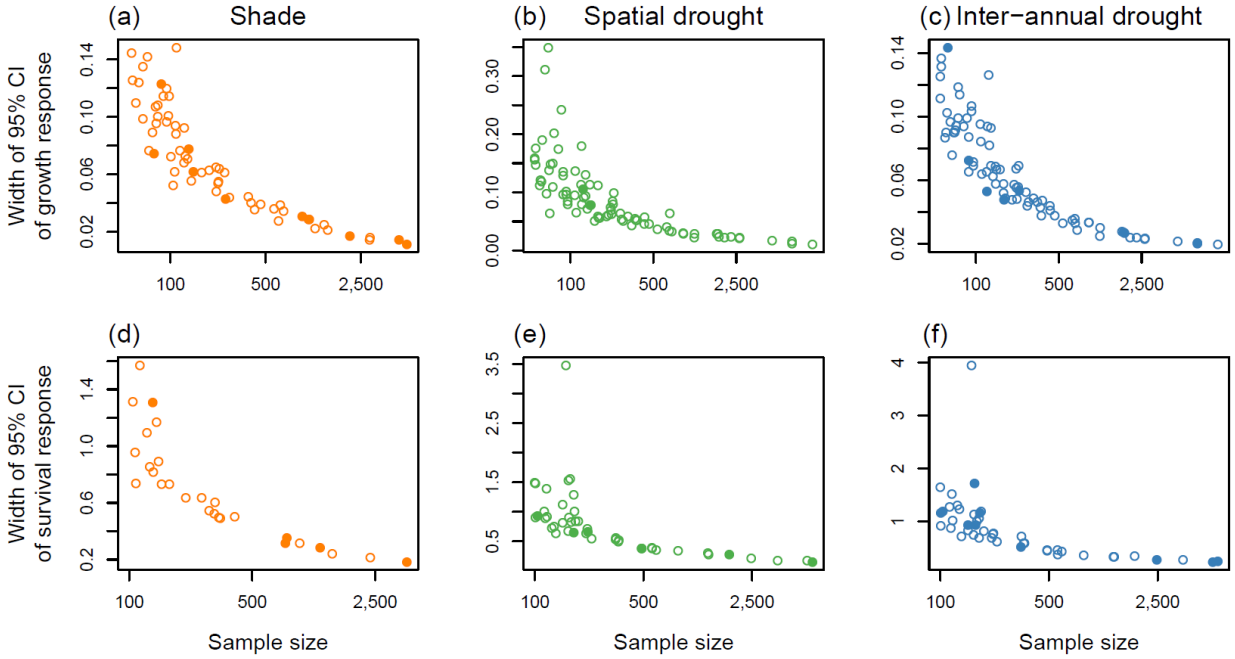


Figure S1.4 Width of the 95% credible interval of growth responses (upper panels) and survival responses (lower panels) of species to shade (a,d), spatial drought (b,e) and inter-annual drought (c,f) versus sample size (i.e. the number of seedling observations of species in the respective models). Filled and unfilled circles represent species with significant and nonsignificant responses, respectively.

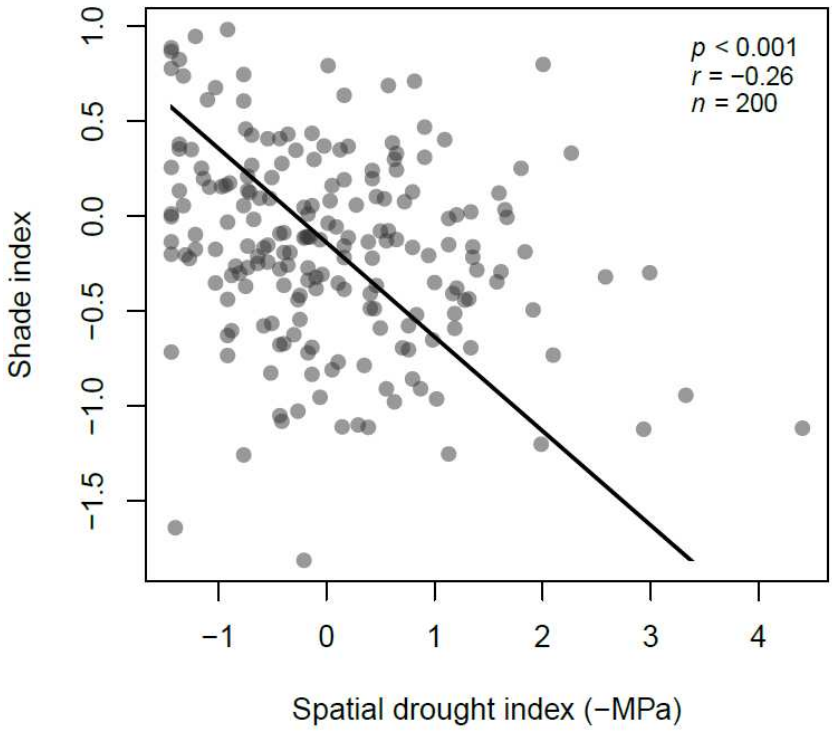


Figure S1.5 Pearson correlation between shade index (means over all years) and spatial drought index at the 200 seedling census sites.

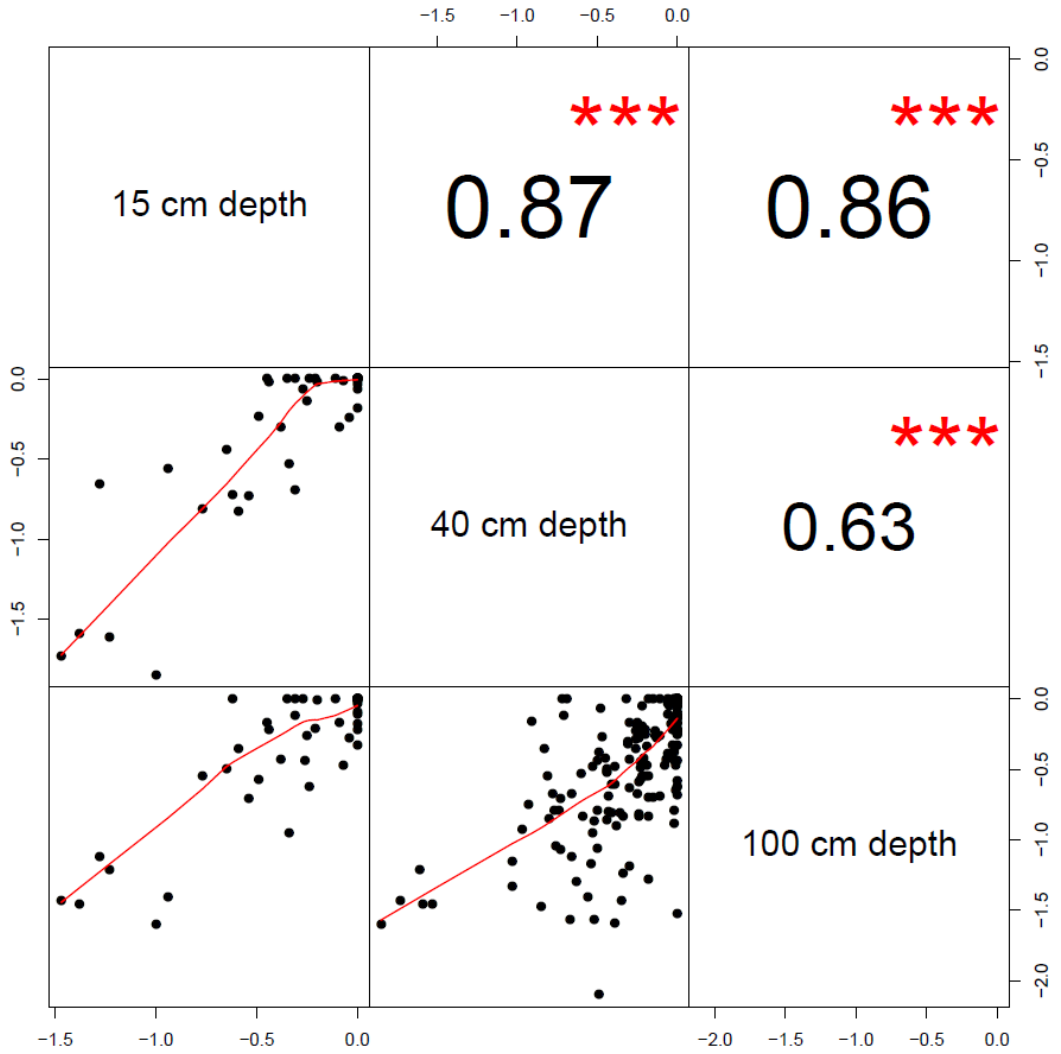


Figure S1.6 Pearson correlations of soil water potentials (MPa) at 15, 40 and 100 cm depth. Samples were taken at 36 seedling census sites and 66 sites along on the border of the 50-ha plot and in a 10-ha plot bordering the full northern side of the 50-ha plot. * All correlations are significant at $p < 0.001$.**

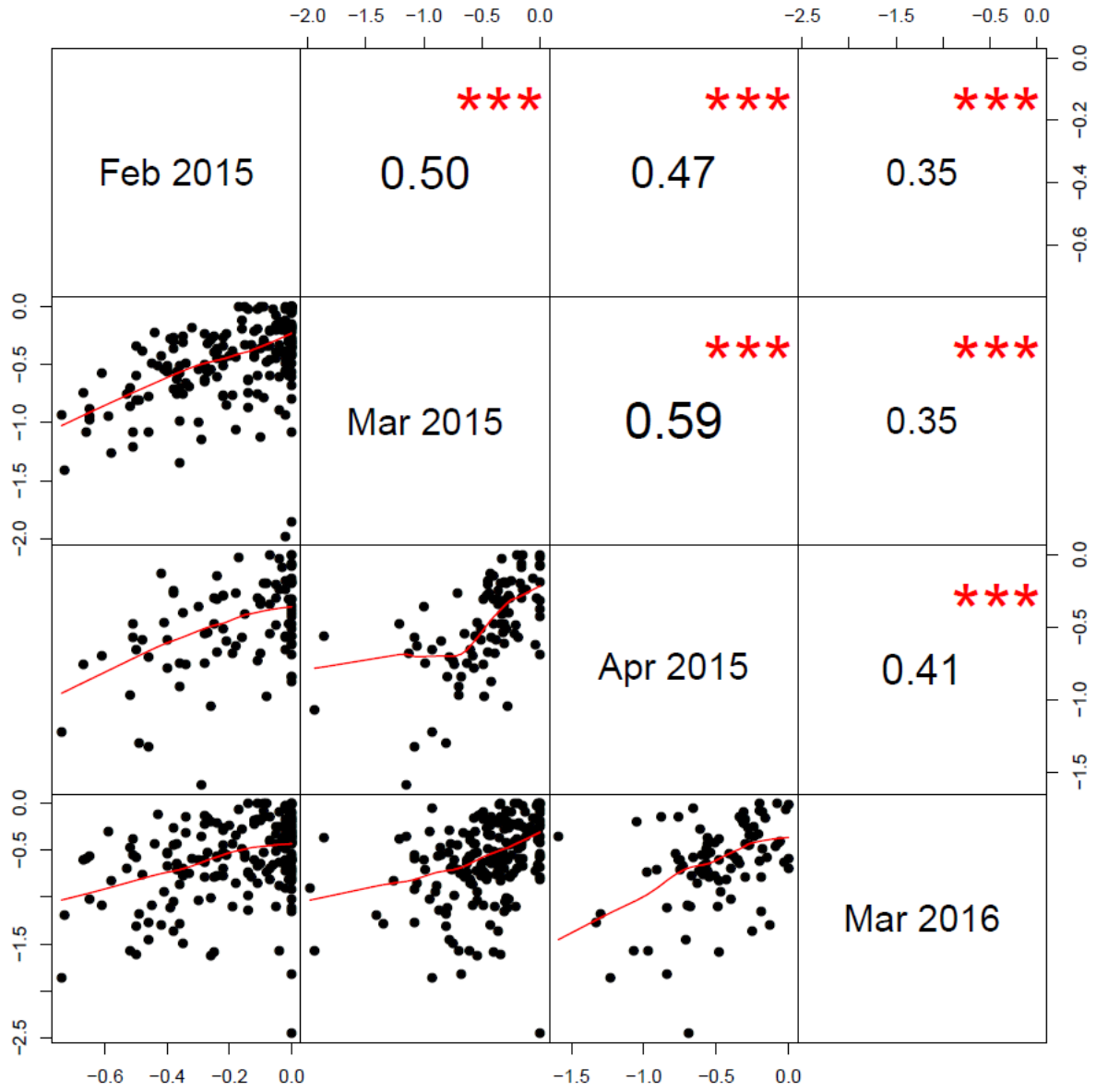


Figure S1.7 Pearson correlations of soil water potentials (MPa) measured at the 200 seedling census sites among the four soil moisture sampling periods. * All correlations are significant at $p < 0.001$.**

Table S1.1 Numbers and percentages of species (in parentheses) with significant growth or survival responses to shade, drought and ln(height).

	Growth responses		Survival responses	
	Negative	**Positive**	**Negative**	**Positive**
Shade (β_1)	9 (16%)	1 (2%)	3 (11%)	2 (7%)
Spatial drought (β_2)	0 (0%)	2 (2%)	4 (9%)	2 (4%)
Inter-annual drought (β_3)	6 (7%)	1 (1%)	10 (22%)	0 (0%)
ln(Height) (β_4)	73 (86%)	0 (0%)	0 (0%)	34 (76%)

Table S1.2 Correlation between shade and drought responses and the fast-slow continuum in the 50-ha plot on BCI[1]. Bold values indicate significant relationships.

Response	Model	Fast-slow axis*	*r*	*p*	*n*
Shade ($\beta_{1,j}$)	Growth	Trees	0.11	0.42	60
		Trees + seedlings	0.09	0.52	60
		Trees + seedlings + seeds	0.05	0.73	50
	Survival	Trees	-0.21	0.31	26
		Trees + seedlings	-0.18	0.38	26
		Trees + seedlings + seeds	-0.21	0.32	24
Spatial drought ($\beta_{2,j}$)	Growth	Trees	0.04	0.70	77
		Trees + seedlings	0.04	0.74	77
		Trees + seedlings + seeds	0.12	0.40	56
	Survival	Trees	0.07	0.66	44
		Trees + seedlings	0.09	0.56	44
		Trees + seedlings + seeds	-0.23	0.20	34
Inter-annual drought ($\beta_{3,j}$)	Growth	Trees	0.07	0.54	77
		Trees + seedlings	0.07	0.55	77
		Trees + seedlings + seeds	0.07	0.61	56
	Survival	Trees	0.46	**0.002**	44
		Trees + seedlings	0.48	**0.001**	44
		Trees + seedlings + seeds	0.45	**0.007**	34

* Trees: recruitment, growth and survival of saplings and trees (≥ 1 cm dbh) in four canopy layers

Seedlings: growth and survival of seedlings (30-100 cm height)

Seeds: Seedling recruitment and seed number

2. Soil water retention curves

To identify outliers in soil water potential (SWP) measurements, we constructed soil water retention curves for 25 of the 200 seedling sites. After measuring SWP of each sample, we determined soil water content (SWC) from fresh mass (f) and dry mass (d) determined after 72 hours at 105°C (SWC = (f–d)/d). We then selected 25 samples from different seedling sites that covered all soil types (cf. Baillie *et al.*[2]) and topographic habitats (cf. Harms *et al.*[3]) of the 50-ha plot to construct soil water retention curves. By selecting sites with different edaphic characteristics, we ensured that the curves represented different possible combinations of SWP and SWC that can be expected at the sites. Thus, substantial deviation from the curves likely indicate measurement error.

To construct the retention curves, we first added distilled water to the soil sample until saturation (0 MPa). The soil was then gradually dried for approximately 30 minutes, weighted and measured for SWP with a WP4C Dewpoint PotentiaMeter (Decagon Devices, Inc, Pullman WA, USA). This was repeated 6-13 times until SWP was lower than -7 MPa. After this, gravimetric SWC was again determined as stated above. Finally, we fitted a third-order polynomial line through the observed SWP vs. SWC to construct each curve, correcting the line to 0 MPa when SWP was predicted to be positive.

To determine SWP outliers, we calculated standard deviation (SD) of the SWC (horizontally) and SWP (vertically) that were measured across all sampling rounds (excluding the observations used to construct the curves). Six SWP samples deviated by more than 1 SD from the most extreme retention curves (Fig. S2.1). These samples were considered outliers and excluded from the analysis. With the remaining samples, we calculated the median SWP per site and multiplied these by -1 to obtain our spatial drought index (D_s).

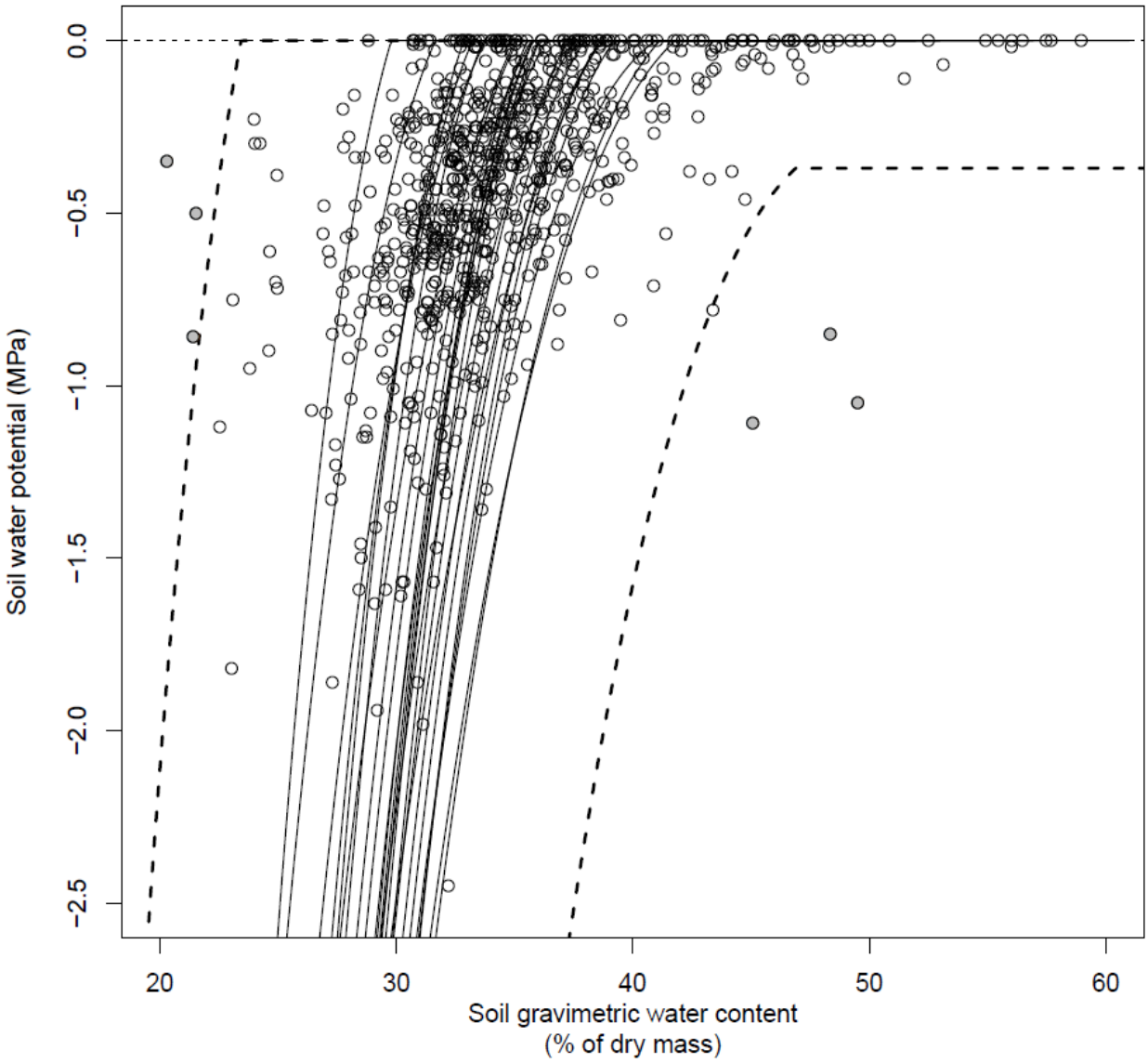


Figure S2.1 Soil water retention curves (solid lines) constructed for 25 of the 200 seedling sites were used to determine outliers in observed SWP and SWC of all measurement rounds (dots). Outliers (grey dots) deviate more than 1 SD from the most extreme curves (dashed lines).

3. Implementation procedures and Stan code

3.1 Model implementation and diagnostics

Posterior distributions and error components were modelled using the Bayesian inference software package RStan version 2.16.2[4] in R version 3.4.1[5]. Convergence was monitored by running four chains with different starting values. We also used the potential scale reduction factor (*Rhat*) to check for convergence of the model. *Rhat* did not exceed 1.1 for any of the parameters in any model, indicating that the models converged[6]. To prevent divergent transitions, we adapted the initial step size, target acceptance rate and maximum treedepth where necessary. We centred and scaled all independent variables to mean 0 and standard deviation 1 to speed up convergence.

Chains of all models that we ran mixed well and converged in less than 100 iterations. For the main models, we used a burn-in period of 1000 iterations and an additional 2,500 iterations after burn-in per chain, giving a total of 10,000 iterations (2500 per chain) for the analyses.

For each model, the proportion of explained variance (R^2) was calculated following Gelman and Hill[6]:

$$R^2 = 1 - \frac{\mathrm{E}(\mathrm{Var}(\epsilon))}{\mathrm{E}(\mathrm{Var}(y))}$$

where *ε* are the model residuals (including all samples after warmup) and *y* are the observed growth or survival of all observations.

3.2 Stan code

Growth model

```
data {
  int<lower=0>                          N_obs;
  int<lower=0>                          N_ind;
  int<lower=0>                          N_year;
  int<lower=0>                          N_sp;
  int<lower=0>                          N_trap;

  vector[N_obs]                         obs;

  vector[N_obs]                         cspatdrought;
  vector[N_obs]                         cinterannualdrought;
  vector[N_obs]                         cshade;
  vector[N_obs]                         clogheight;

  int<lower=0>                          species[N_obs];
  int<lower=0>                          ind[N_obs];
  int<lower=0>                          spind[N_ind];
  int<lower=0>                          repind[N_ind];

  int<lower=0>                          year[N_obs];
  int<lower=0>                          trap[N_obs];
}
parameters {
  vector<lower=-10,upper=10>[N_sp]      b0;
  vector<lower=-10,upper=10>[N_sp]      b1;
  vector<lower=-10,upper=10>[N_sp]      b2;
  vector<lower=-10,upper=10>[N_sp]      b3;
  vector<lower=-10,upper=10>[N_sp]      b4;

  vector<lower=-10,upper=10>[N_year]    a_year;
  vector<lower=-10,upper=10>[N_ind]     a_ind;
  vector<lower=-10,upper=10>[N_trap]     a_trap;

//hyperparameters
  vector<lower=0,upper=2>[N_sp]         sigma_p;
  vector<lower=0,upper=2>[N_sp]         sigma_aind;

  real<lower=0,upper=2>                 sigma_year;
  real<lower=0,upper=2>                 sigma_trap;
  real<lower=0,upper=2>                 sigma_sigp;
  real<lower=0,upper=2>                 sigma_sigaind;
}
model{
  vector[N_obs]                         pred;

  a_trap ~ normal(0,sigma_trap);
  a_year ~ normal(0,sigma_year);

  for( i in 1:N_ind){
    if(repind[i] == 1){
      a_ind[i] ~ normal(0,sigma_aind[spind[i]]);
    }
```

```
  }

  sigma_aind ~ normal(mu_sigaind, sigma_sigaind);
  sigma_p ~ normal(mu_sigp,sigma_sigp);


   for( i in 1:N_obs ){
          if(cshade[i]==-9){
                    if( repind[ind[i]] == 1 ){
                              pred[i] = a_ind[ind[i]] + a_year[year[i]] + a_trap[trap[i]] + b0[species[i]] +
                                                  b2[species[i]] * cspatdrought[i] +
                              b3[species[i]] * cinterannualdrought[i] + b4[species[i]] * clogheight[i];
                    }
                    else{
                              pred[i] =                    a_year[year[i]] + a_trap[trap[i]] + b0 [species[i]] +
                                                  b2[species[i]] * cspatdrought[i] +
                              b3[species[i]] * cinterannualdrought[i] + b4[species[i]] * clogheight[i];
                    }
          }
          else{
             if( repind[ind[i]] == 1 ){
                              pred[i] = a_ind[ind[i]] + a_year[year[i]] + a_trap[trap[i]] + b0[species[i]] +
                              b1[species[i]] * cshade[i] + b2[species[i]] * cspatdrought[i] +
                              b3[species[i]] * cinterannualdrought[i] + b4[species[i]] * clogheight[i];
                    }
                    else{
                              pred[i] =                   a_year[year[i]] + a_trap[trap[i]] + b0[species[i]] +
                              b1[species[i]] * cshade[i] + b2[species[i]] * cspatdrought[i] +
                              b3[species[i]] * cinterannualdrought[i] + b4[species[i]] * clogheight[i];
                    }
           }
          obs[i] ~ normal(pred[i], sigma_p[species[i]]);
          }
}
```

Survival model

```
data {
  int<lower=0>                    N_ind;
  int<lower=0>                    N_year;
  int<lower=0>                    N_trap;
  int<lower=0>                    N_sp;

  int<lower=0,upper=1>            alive[N_ind];

  vector[N_ind]                   cspatdrought;
  vector[N_ind]                   cinterannualdrought;
  vector[N_ind]                   cshade;
  vector[N_ind]                   clogheight;

  int<lower=0>                    species[N_ind];
  int<lower=0>                    year[N_ind];
  int<lower=0>                    trap[N_ind];
}
parameters {
  real<lower=-10,upper=10>        b0[N_sp];
  real<lower=-10,upper=10>        b1[N_sp];
  real<lower=-10,upper=10>        b2[N_sp];
  real<lower=-10,upper=10>        b3[N_sp];
  real<lower=-10,upper=10>        b4N_sp];

  real<lower=-10,upper=10>        a_year[N_year];
  real<lower=-10,upper=10>        a_trap[N_trap];

//hyperparameters
  real<lower=0,upper=2>           sigma_year;
  real<lower=0,upper=2>           sigma_trap;
}
transformed parameters {
vector[N_ind]                     theta;
  real s;

  for (i in 1:N_ind){
          if(cshade[i]==-9){
                  s[i] =  a_year[year[i]] + a_trap[trap[i]] + b0[species[i]] +
                  b2[species[i]] * cspatdrought[i] + b3[species[i]] * cinterannualdrought[i] +
                  b4[species[i]] * clogheight[i];
    }else{
                  s[i] =  a_year[year[i]] + a_trap[trap[i]] + b0[species[i]] + b1[species[i]] * cshade[i] +
                  b2[species[i]] * cspatdrought[i] + b3[species[i]] * cinterannualdrought[i] +
                  b4[species[i]] * clogheight[i];
          }
          theta[i] = 1/(1+exp(-s));
  }
}
model {
  for(i in 1:N_trap){
```

```
        a_trap[i] ~ normal(0,sigma_trap);
        }

  for(i in 1:N_year){
        a_year[i] ~ normal(0,sigma_year);
        }

  for (i in 1:N_ind){
    alive[i] ~ bernoulli(theta[i]);
  }
}
```

References

1 Rüger, N. *et al.* Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. *Ecology Letters* **21**, 1075-1084 (2018).

2 Baillie, I., Elsenbeer, H., Barthold, F., Grimm, R. & Stallard, R. Semi-detailed soil survey of Barro Colorado Island, Panama. 54 pp., https://biogeodb.stri.si.edu/bioinformatics/bci_soil_map/ (Smithsonian Tropical Research Institute, 2007).

3 Harms, K. E., Condit, R., Hubbell, S. P. & Foster, R. B. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology* **89**, 947-959 (2001).

4 Stan Development Team. RStan: the R interface to Stan, version 2.16.2. http://mc-stan.org (2017).

5 R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria, https://www.R-project.org/ (2017).

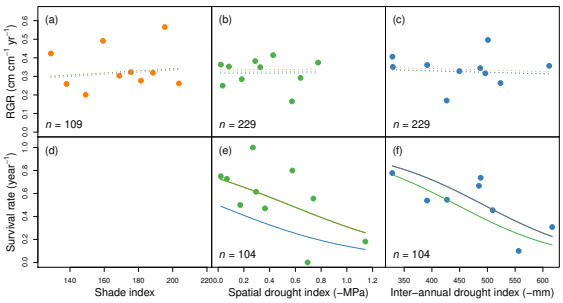
6 Gelman, A. & Hill, J. Data analysis using regression and multilevel/hierarchical models. 625 pp. (Cambridge University Press, 2007).

4. All species responses

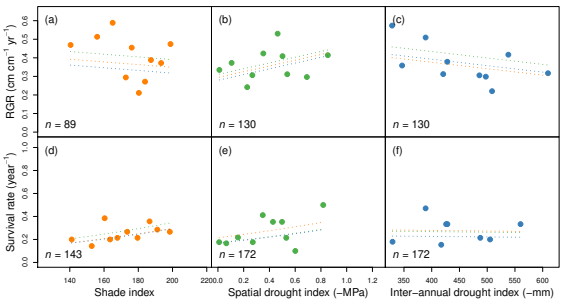
Here we provide Figure S1, which visualises all species responses to shade and drought. We also provide Tables S1-S2 with the parameter estimates and 95% credible intervals for all species.

Figure S1 The following pages show observed and fitted relative growth rate (RGR, upper panels) and survival rate (lower panels) against shade (a,d), spatial drought (b,e) and inter-annual drought (c,f) for all species at their mean seedling height. Solid and dotted lines indicate significant and non-significant responses of species to shade or drought, respectively. Large dots represent mean observed growth or survival for ten shade or drought classes, each containing 10% of the individuals of the species (fewer than 10 dots indicate that a species occurs in a limited set of sites or years). Lines show fitted growth and survival with increasing shade (a,d, red), spatial drought (b,e, yellow) and inter-annual drought (c,f, blue), at mean values of the other predictors. Lines with a different colour than the large dots represent 1 SD increase in shade (red), spatial drought (yellow) or inter-annual drought (blue). Panels without data indicate that a species did not reach the selection criteria for that particular relationship (see *Methods: Estimating shade and drought responses*).

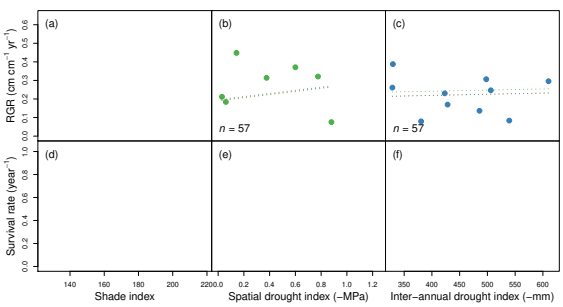
Acalypha diversifolia



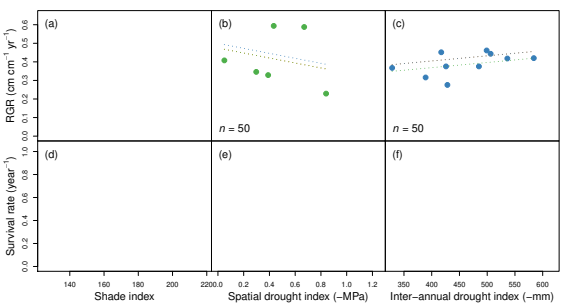
Aegiphila panamensis



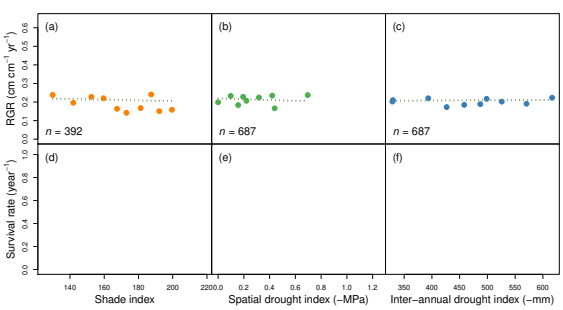
Alibertia edulis



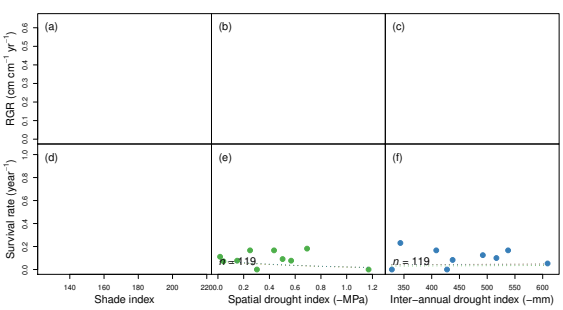
Allophylus psilospermus



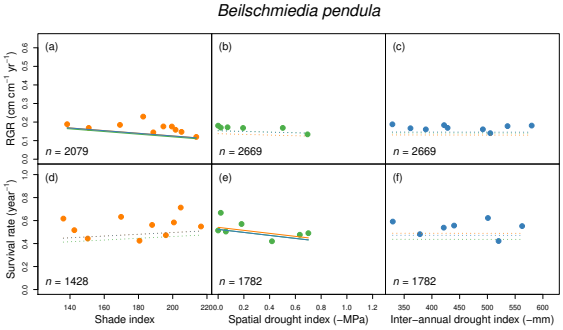
Alseis blackiana



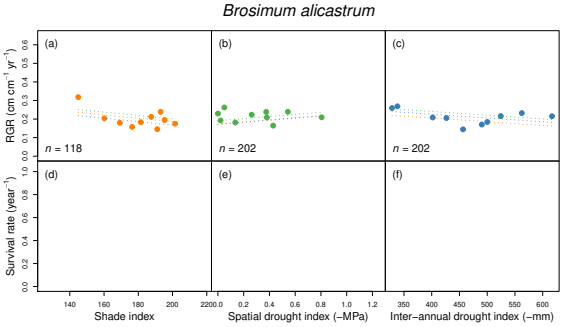
Apeiba membranacea



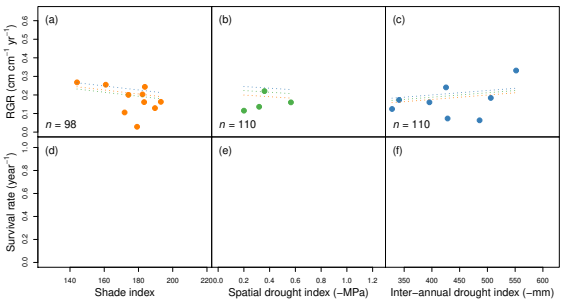
Beilschmiedia pendula



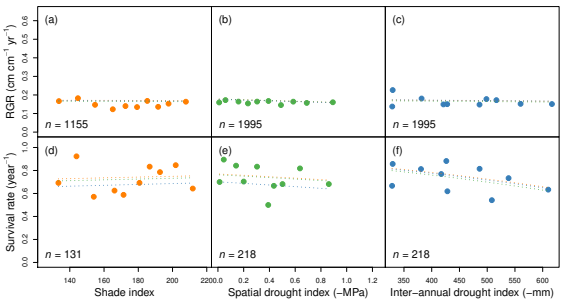
Brosimum alicastrum



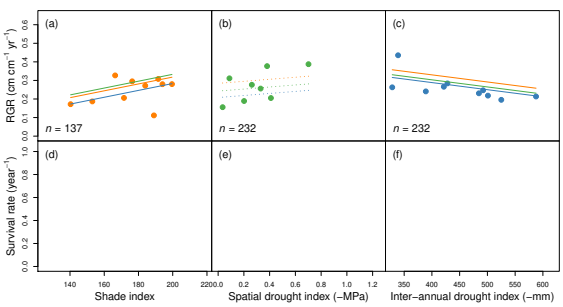
Calophyllum longifolium



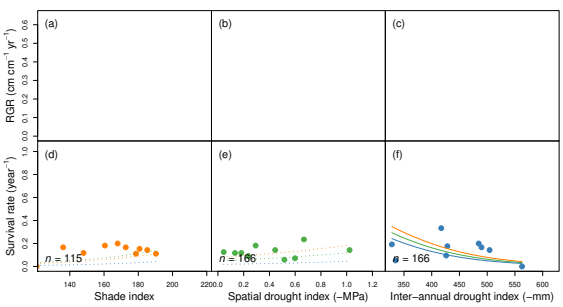
Capparis frondosa



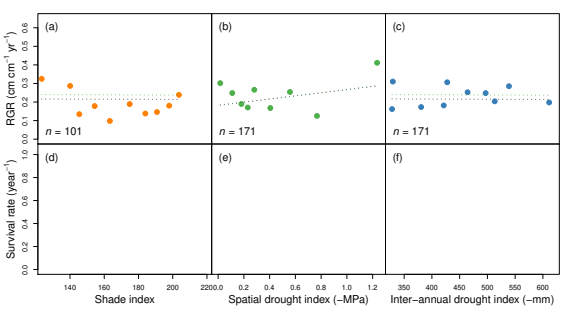
Cassipourea elliptica



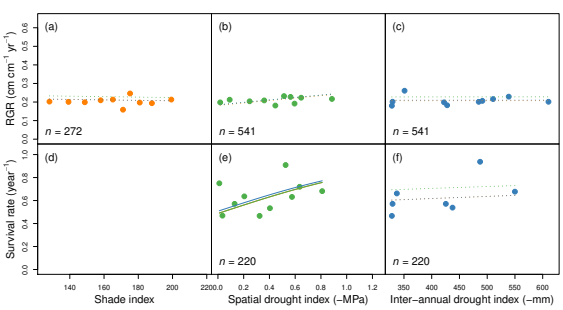
Cecropia insignis



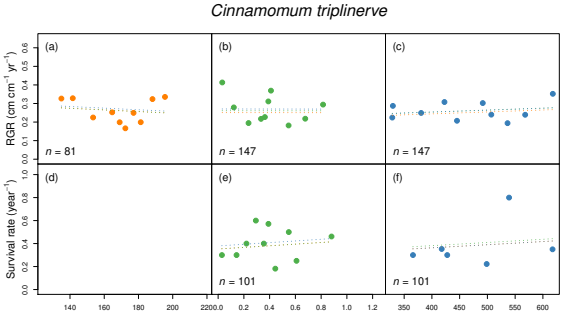
Chrysophyllum argenteum



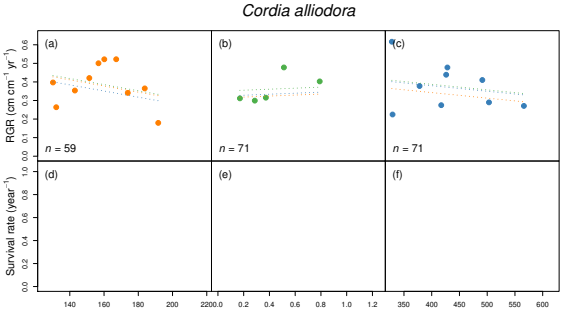
Chrysophyllum cainito



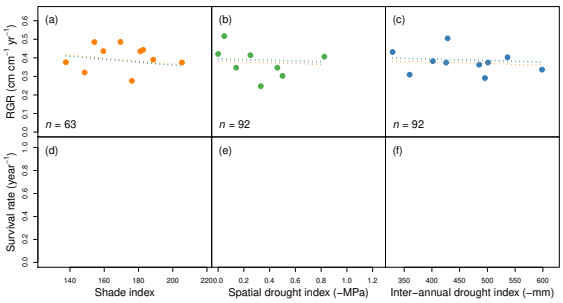
Cinnamomum triplinerve



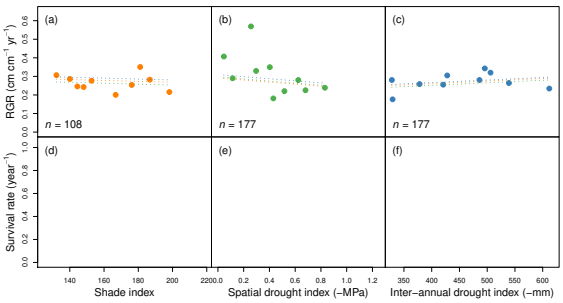
Cordia alliodora



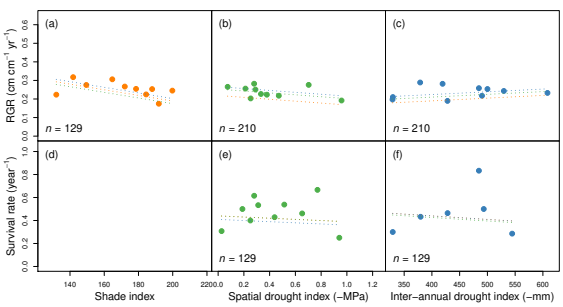
Cordia bicolor



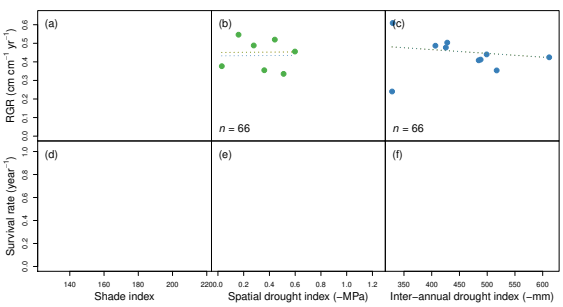
Cordia lasiocalyx



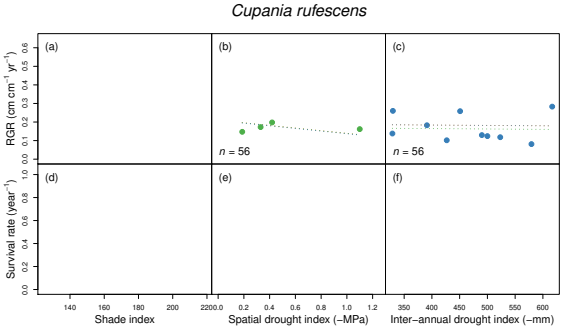
Coussarea curvigemmia



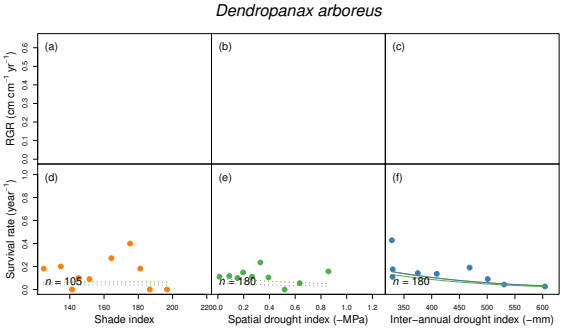
Croton billbergianus



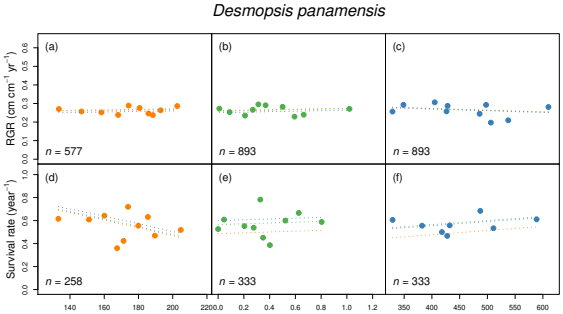
Cupania rufescens



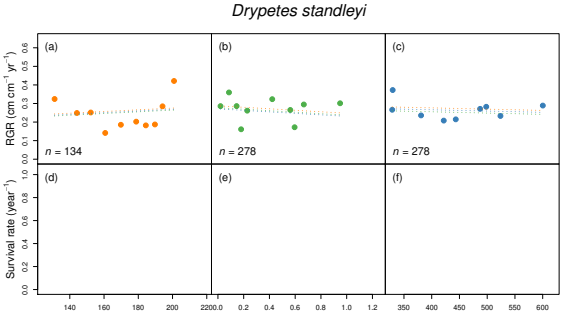
Dendropanax arboreus



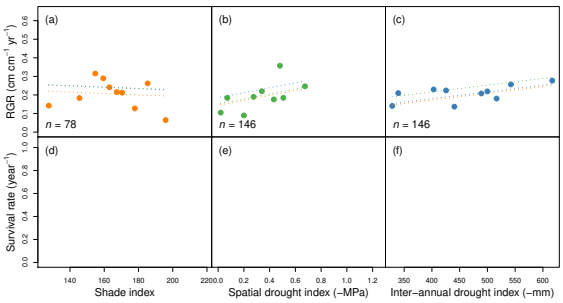
Desmopsis panamensis



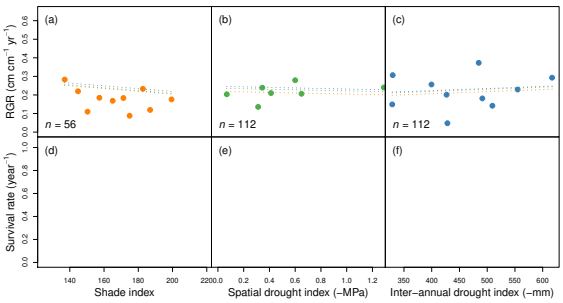
Drypetes standleyi



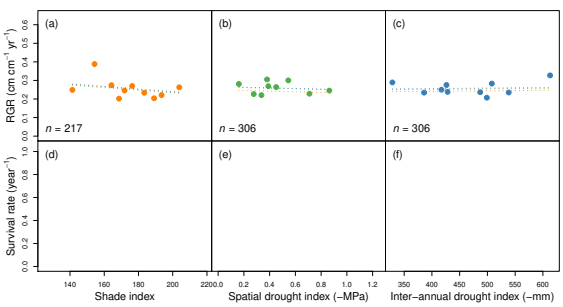
Erythroxylum macrophyllum



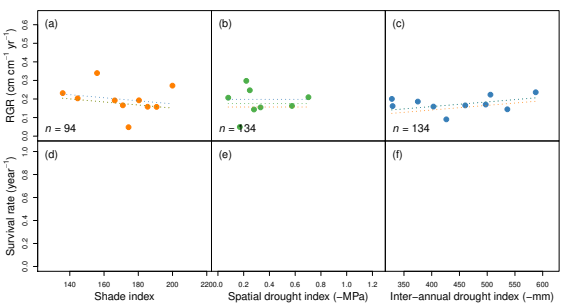
Eugenia coloradoensis



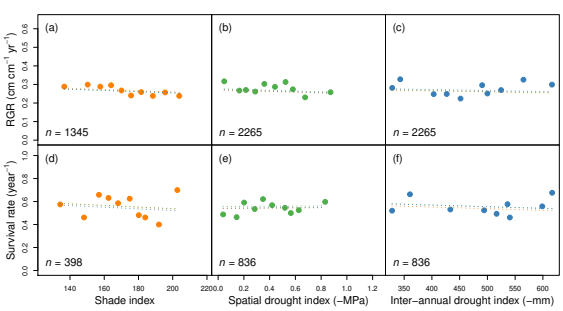
Eugenia galalonensis



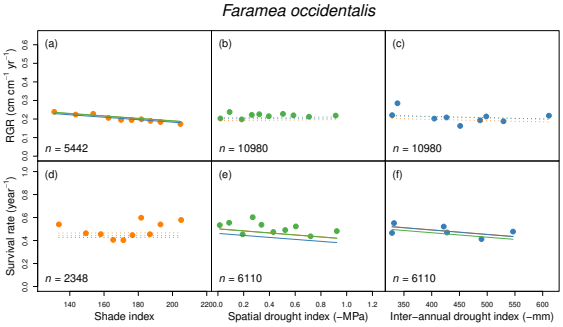
Eugenia nesiotica



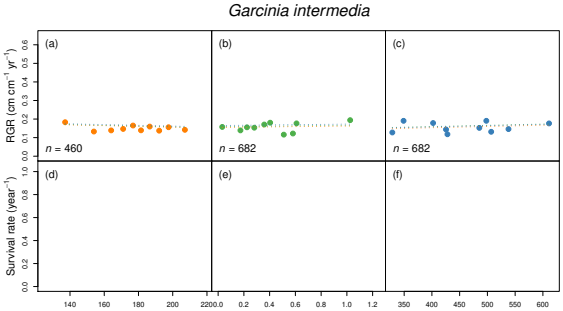
Eugenia oerstediana



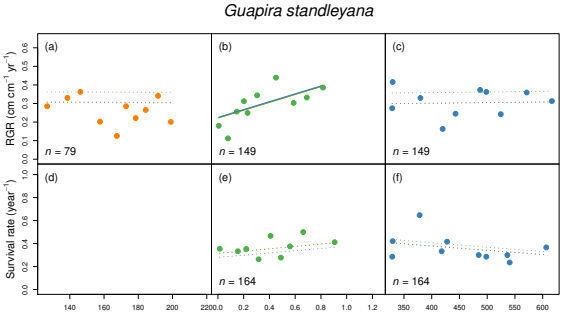
Faramea occidentalis

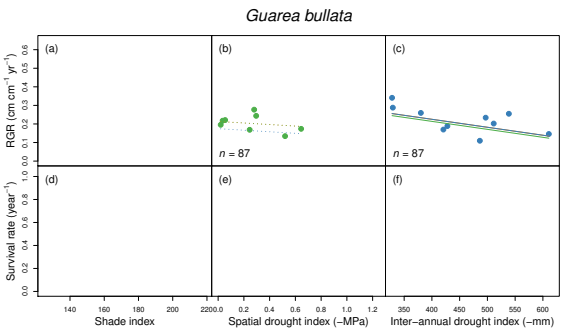


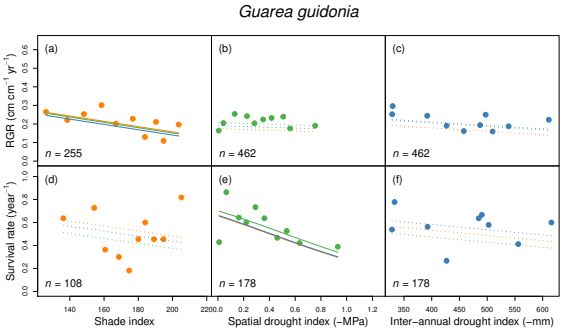
Garcinia intermedia

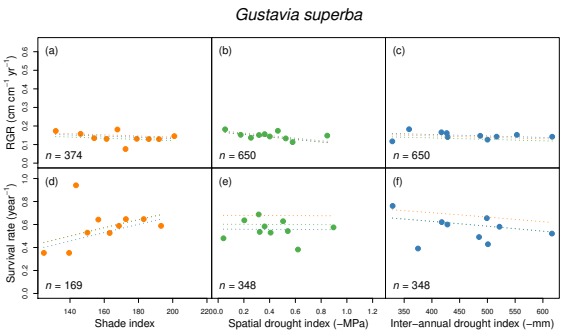


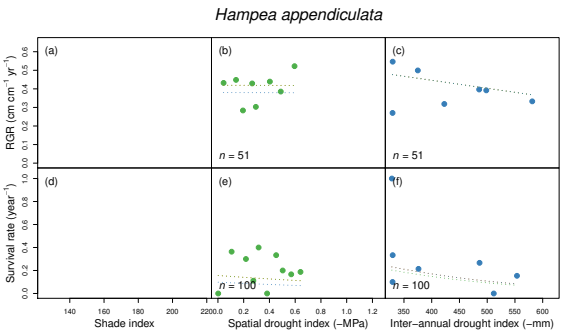
Guapira standleyana

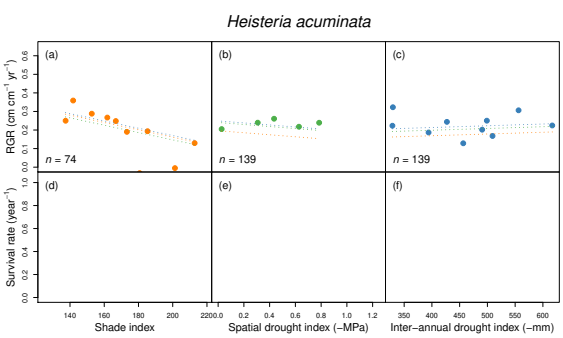


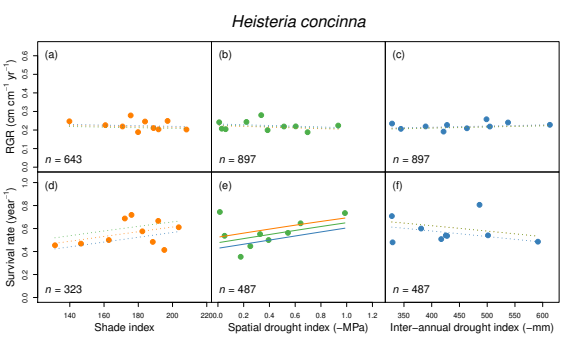

Guarea bullata
(a)
(b)
(c)
(d)
(e)
(f)
n = 87
n = 87
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)

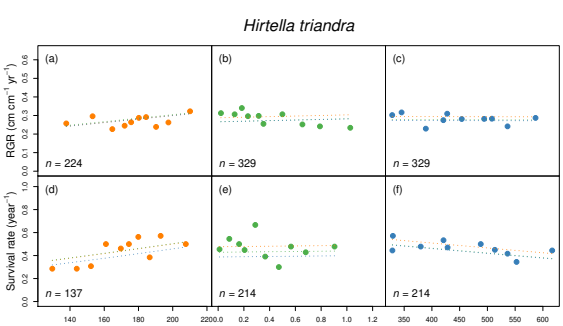

Guarea guidonia
(a)
(b)
(c)
(d)
(e)
(f)
n = 255
n = 462
n = 462
n = 108
n = 178
n = 178
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)

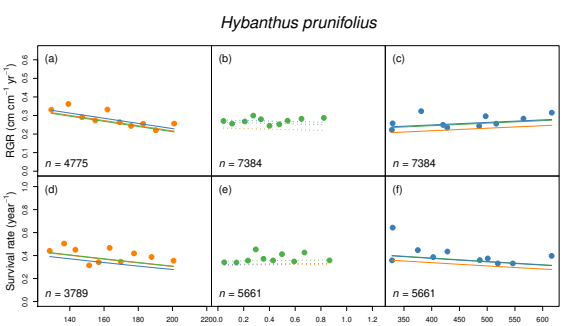

Gustavia superba
(a)
(b)
(c)
(d)
(e)
(f)
n = 374
n = 650
n = 650
n = 169
n = 348
n = 348
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)


Hampea appendiculata
(a)
(b)
(c)
(d)
(e)
(f)
n = 51
n = 51
n = 100
n = 100
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)

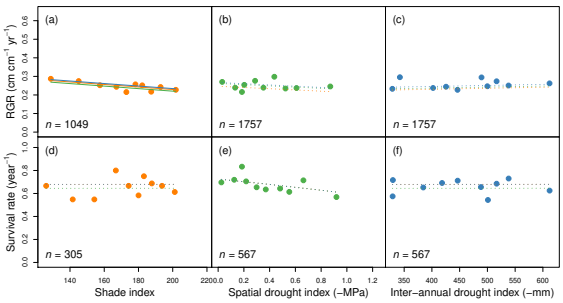

Heisteria acuminata
(a)
(b)
(c)
(d)
(e)
(f)
n = 74
n = 139
n = 139
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)


Heisteria concinna
(a)
(b)
(c)
(d)
(e)
(f)
n = 643
n = 897
n = 897
n = 323
n = 487
n = 487
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)

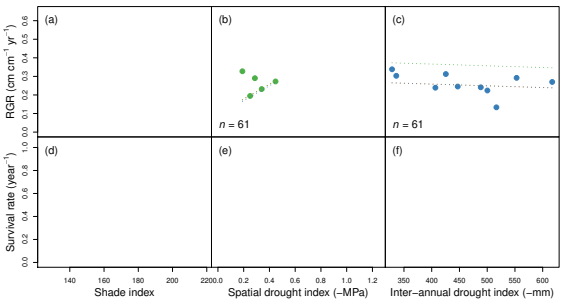

Hirtella triandra
(a)
(b)
(c)
(d)
(e)
(f)
n = 224
n = 329
n = 329
n = 137
n = 214
n = 214
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)


Hybanthus prunifolius
(a)
(b)
(c)
(d)
(e)
(f)
n = 4775
n = 7384
n = 7384
n = 3789
n = 5661
n = 5661
RGR (cm cm⁻¹ yr⁻¹)
Survival rate (year⁻¹)
Shade index
Spatial drought index (–MPa)
Inter–annual drought index (–mm)

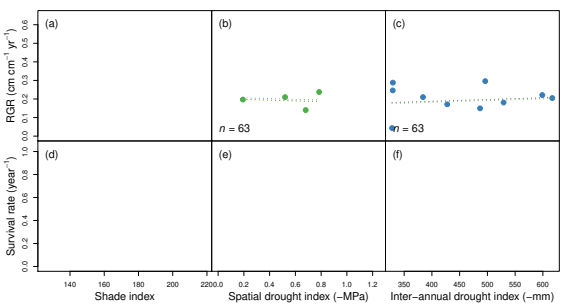
Inga marginata



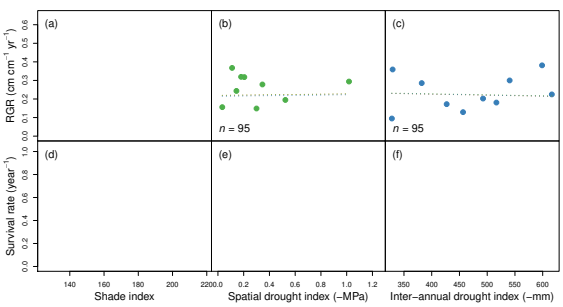
Inga multijuga



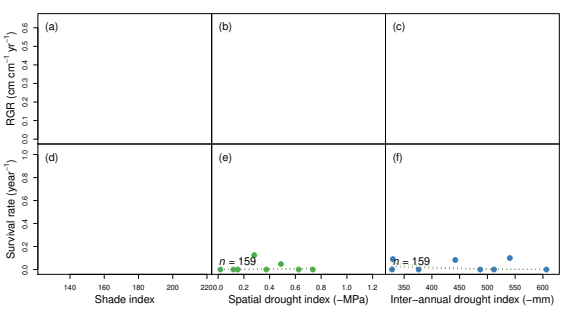
Inga nobilis



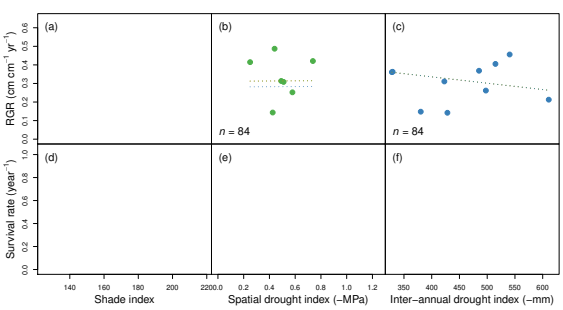
Inga umbellifera



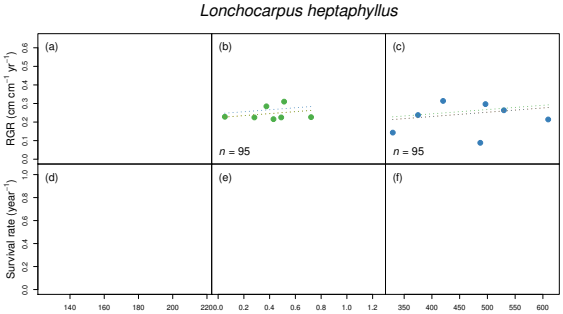
Jacaranda copaia



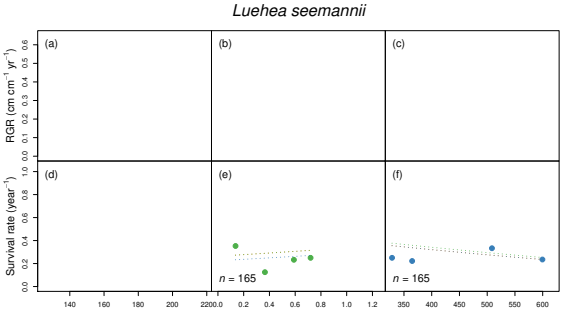
Lacistema aggregatum



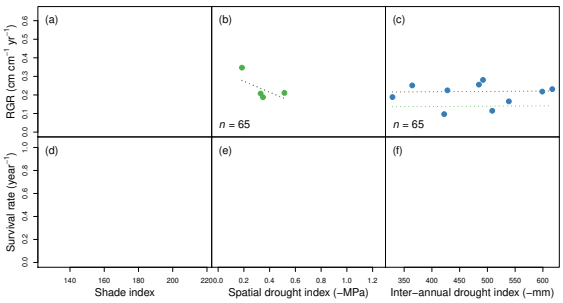
Lonchocarpus heptaphyllus



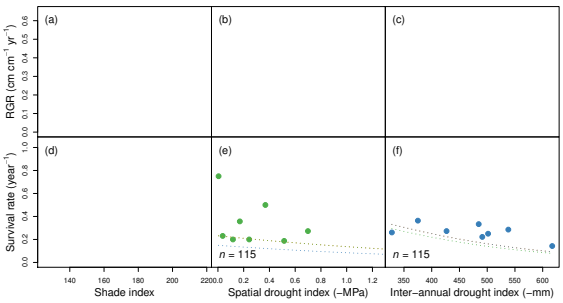
Luehea seemannii



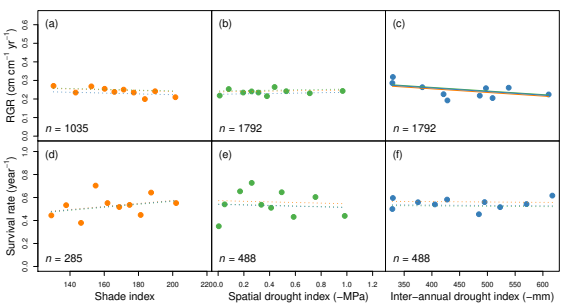
Malpighia romeroana



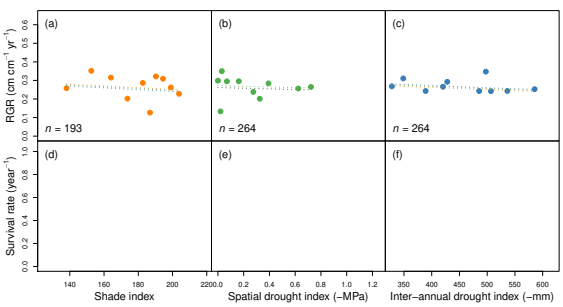
Miconia argentea



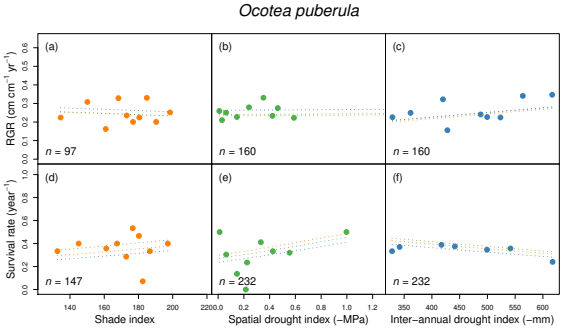
Mouriri myrtilloides



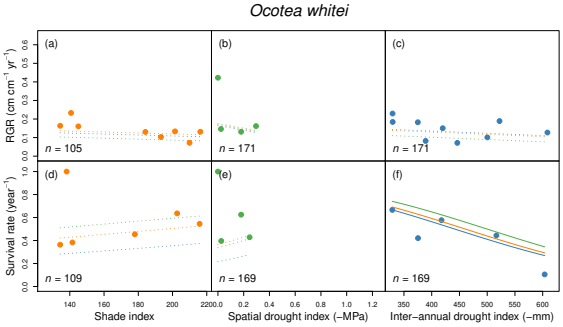
Nectandra lineata



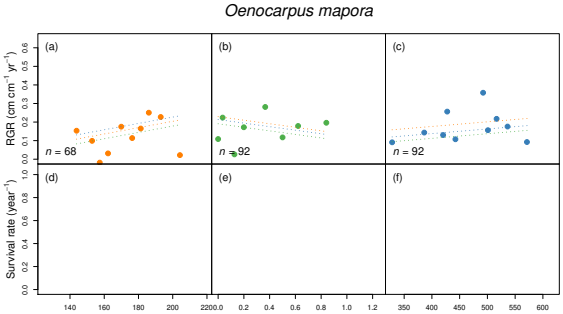
Ocotea puberula



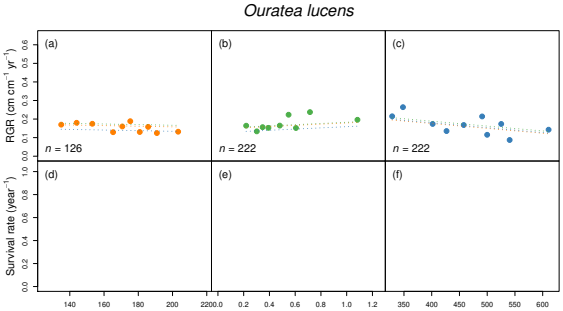
Ocotea whitei



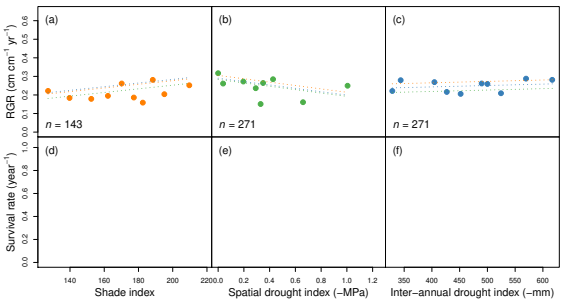
Oenocarpus mapora



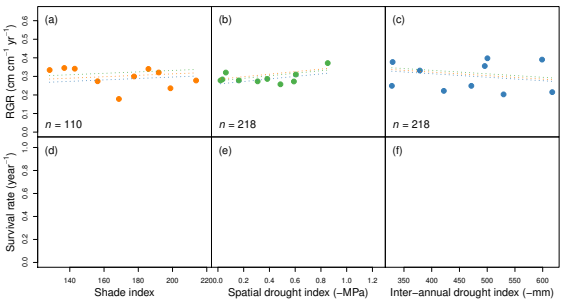
Ouratea lucens



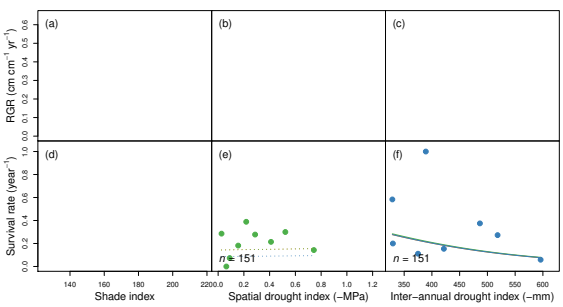
Picramnia latifolia



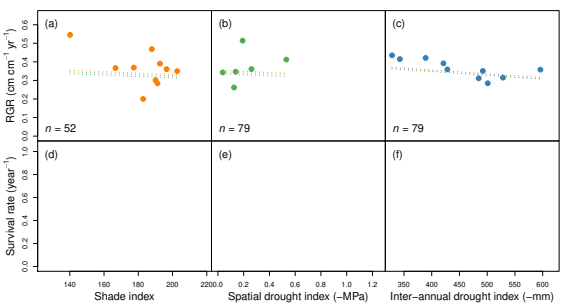
Piper darienense



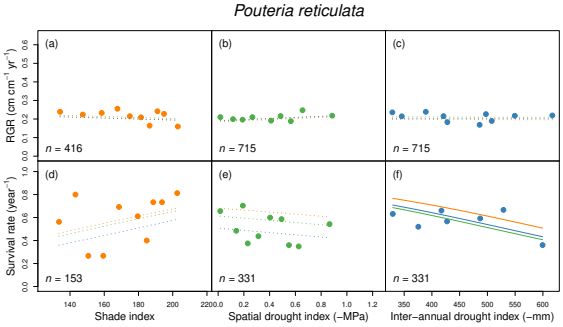
Piper reticulatum



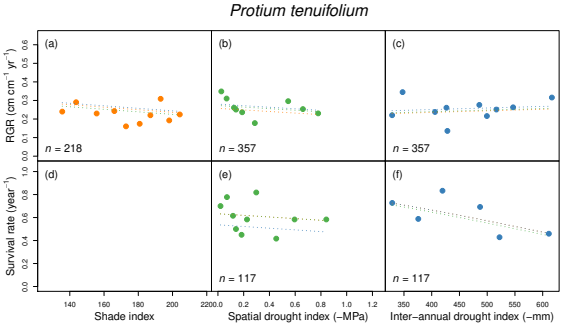
Poulsenia armata



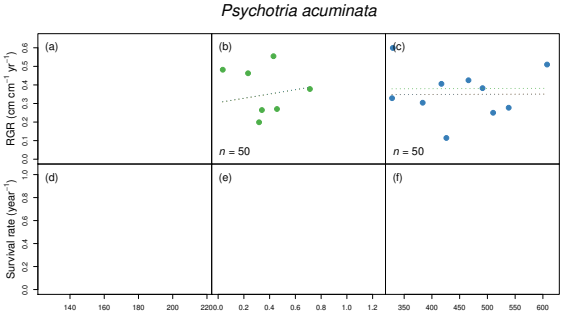
Pouteria reticulata



Protium tenuifolium



Psychotria acuminata



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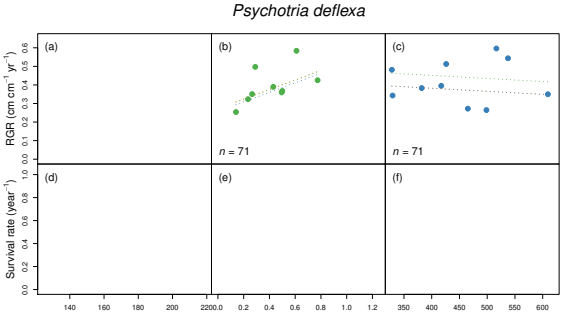

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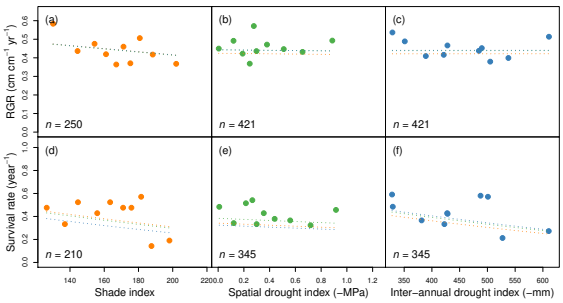

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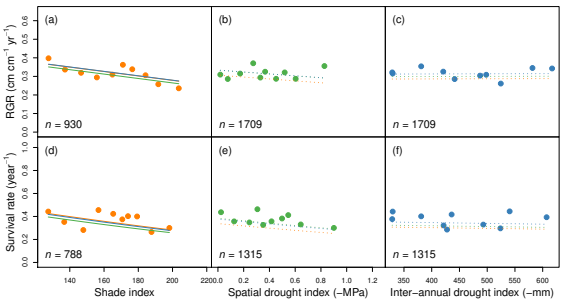

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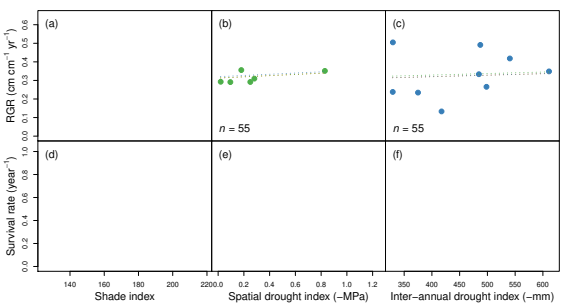

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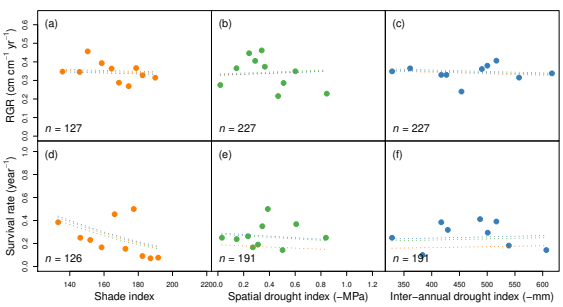

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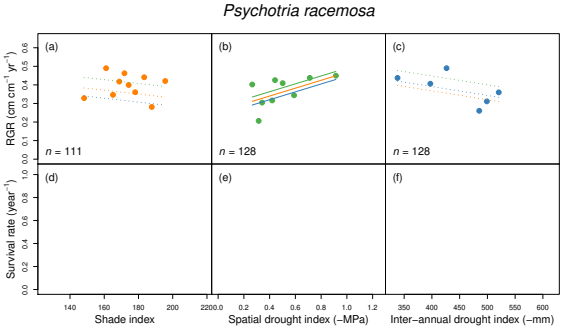

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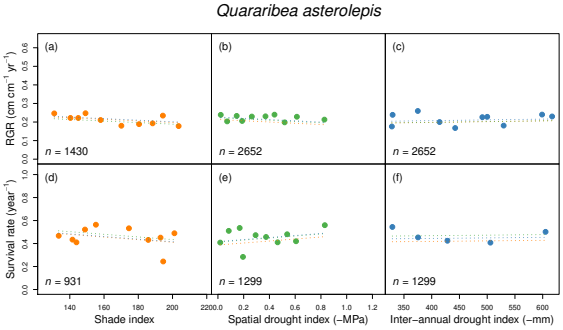

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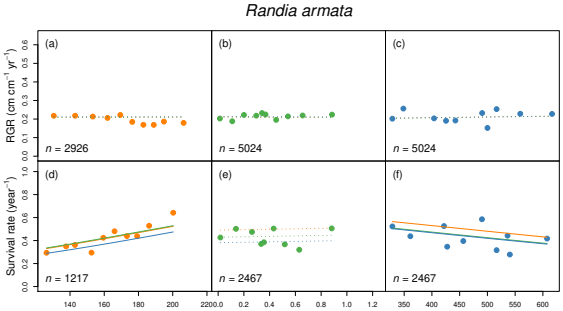

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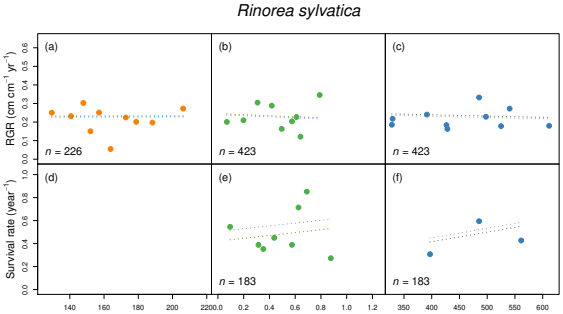

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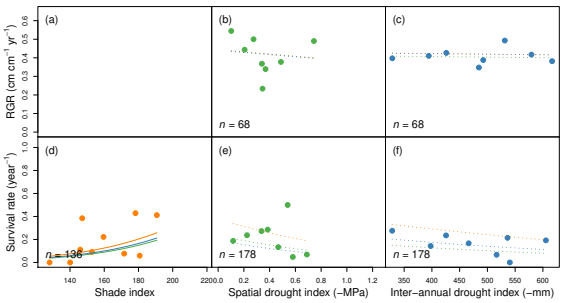
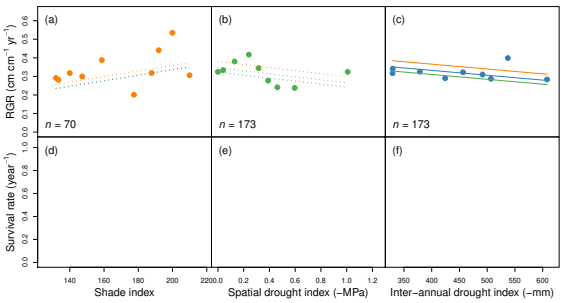


Simarouba amara



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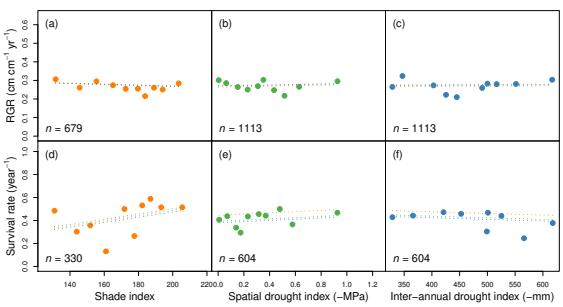

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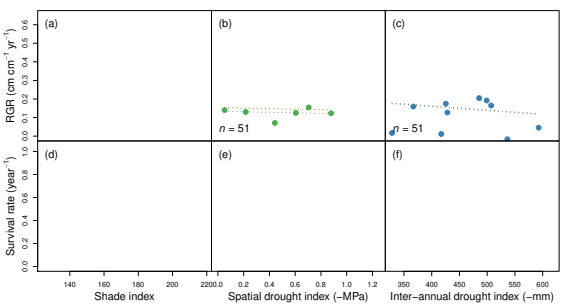

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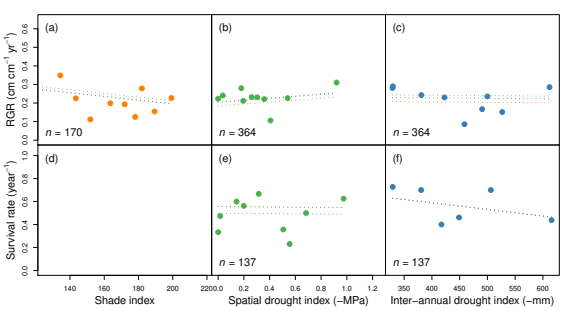
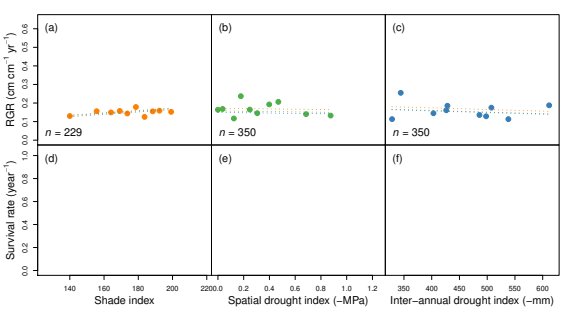


Swartzia simplex_var.grandiflora



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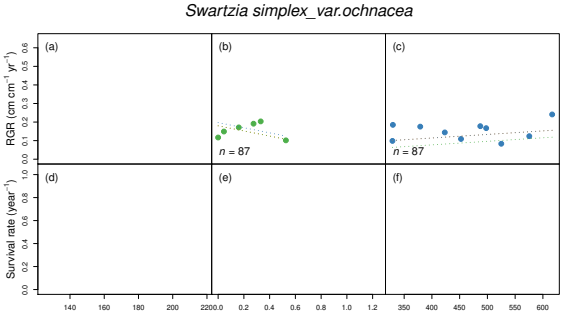

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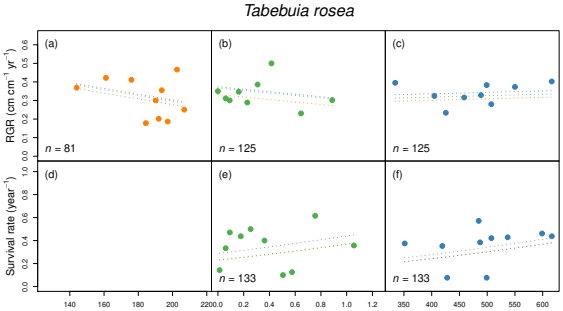

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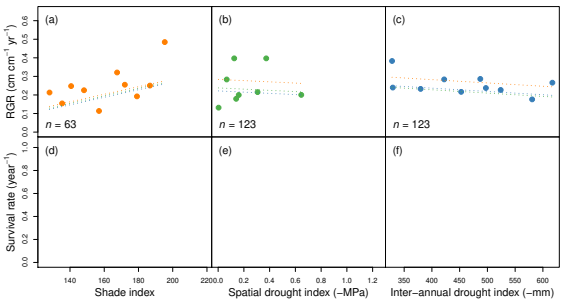

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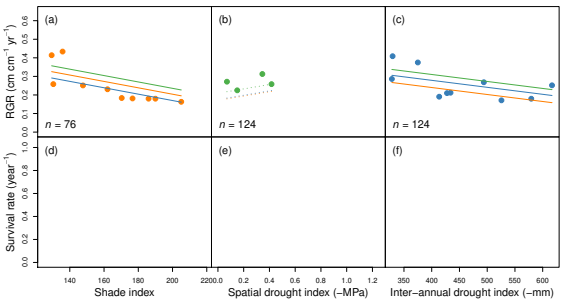

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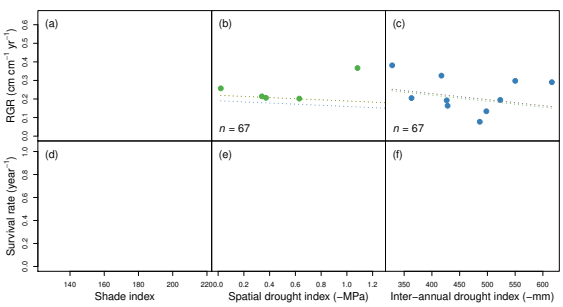

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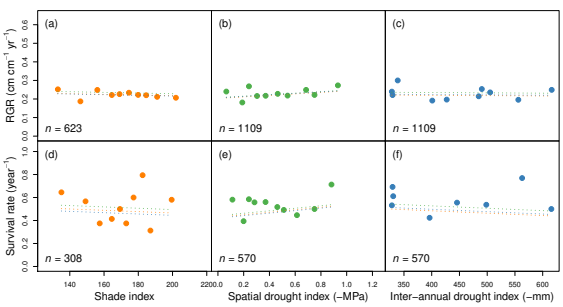
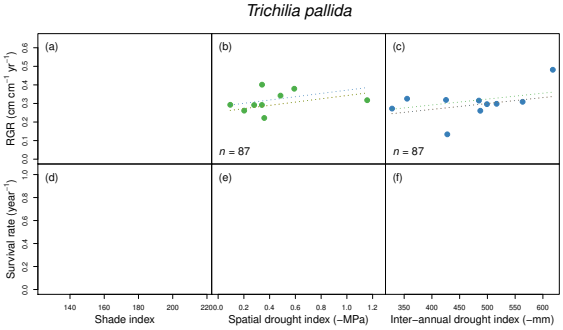
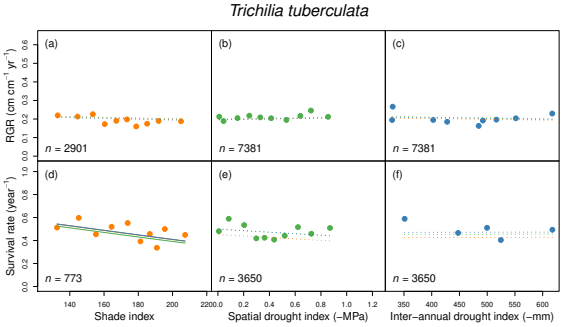


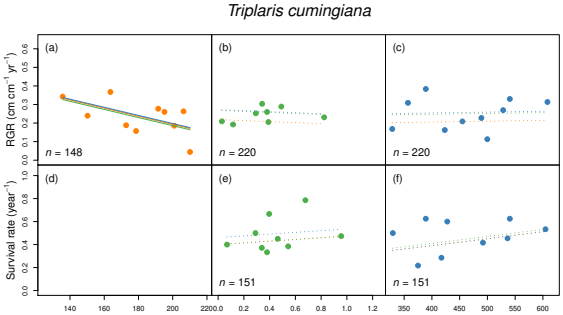
Trichilia pallida



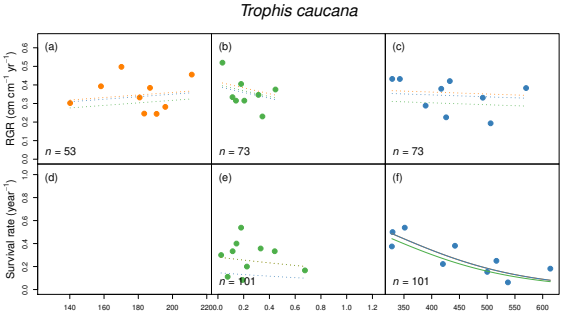
Trichilia tuberculata



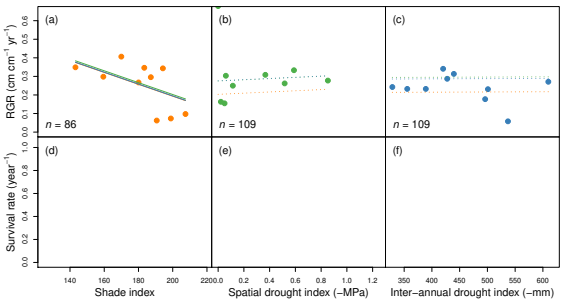
Triplaris cumingiana



Trophis caucana



Unonopsis pittieri



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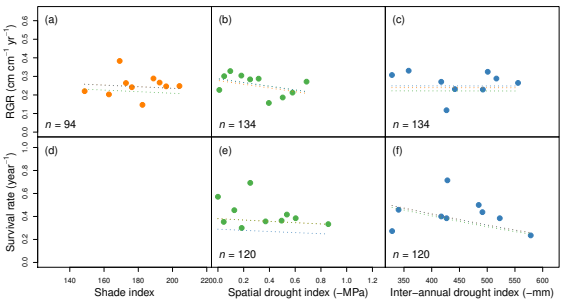

Vochysia ferruginea

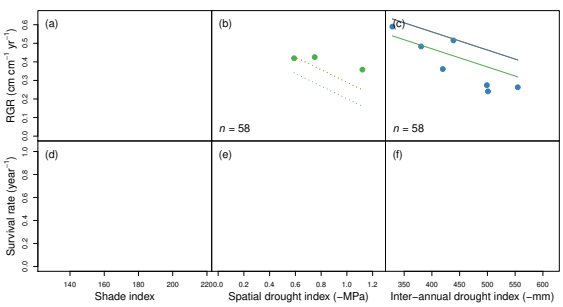

Table S1 Mean and 95% CI of responses in terms of relative growth rates to shade (β1), spatial drought (β2) and inter-annual drought (β3) for all species. Further shown are the number of observations of a species in years with and without shade estimates, mean RGR (β0) and the response to ln(height) (β4). Bold and underlined values indicate significant responses to shade or drought, i.e. the 95% credible interval (CI) excluded zero. Underlined values indicate that the CI of β0 or β4 excluded zero.

	Observations		Mean RGR (β0)			Shade (β1)			Spatial drought (β2)			Int.-an. drought (β3)			ln(height) (β4)		
Species	all	shade	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+
Acalypha diversifolia	229	109	0.264	0.305	0.346	-0.034	0.013	0.060	-0.038	0.001	0.042	-0.042	-0.007	0.028	-0.088	-0.059	-0.032
Aegiphila panamensis	130	89	0.323	0.366	0.410	-0.073	-0.016	0.042	-0.004	0.041	0.087	-0.072	-0.031	0.009	-0.162	-0.128	-0.094
Alibertia edulis	57	33	0.219	0.291	0.363				-0.036	0.023	0.082	-0.046	0.006	0.056	-0.152	-0.101	-0.052
Allophylus psilospermus	50	37	0.351	0.424	0.499				-0.115	-0.036	0.041	-0.038	0.025	0.088	-0.074	-0.022	0.031
Alseis blackiana	687	392	0.245	0.273	0.304	-0.024	-0.004	0.016	-0.038	-0.006	0.027	-0.015	0.002	0.018	-0.100	-0.083	-0.065
Beilschmiedia pendula	2669	2079	0.163	0.181	0.199	**-0.024**	**-0.016**	**-0.008**	-0.017	-0.005	0.006	-0.012	0.000	0.012	-0.060	-0.043	-0.027
Brosimum alicastrum	202	118	0.246	0.290	0.334	-0.058	-0.020	0.019	-0.014	0.015	0.045	-0.042	-0.018	0.006	-0.149	-0.101	-0.053
Calophyllum longifolium	110	98	0.246	0.311	0.376	-0.082	-0.024	0.033	-0.081	-0.012	0.056	-0.020	0.022	0.064	-0.246	-0.161	-0.073
Capparis frondosa	1995	1155	0.180	0.195	0.210	-0.012	-0.001	0.010	-0.017	-0.005	0.006	-0.014	-0.002	0.010	-0.120	-0.105	-0.090
Cassipourea elliptica	232	137	0.216	0.257	0.297	**0.002**	**0.042**	**0.080**	-0.035	0.015	0.064	**-0.062**	**-0.035**	**-0.008**	-0.131	-0.105	-0.080
Chrysophyllum argenteum	171	101	0.193	0.236	0.278	-0.037	-0.001	0.036	-0.007	0.023	0.052	-0.030	-0.001	0.028	-0.092	-0.055	-0.018
Chrysophyllum cainito	541	272	0.189	0.209	0.229	-0.025	-0.003	0.019	-0.001	0.018	0.036	-0.016	0.000	0.017	-0.108	-0.083	-0.060
Cinnamomum triplinerve	147	81	0.224	0.261	0.299	-0.060	-0.010	0.040	-0.039	0.000	0.039	-0.019	0.009	0.039	-0.058	-0.003	0.051
Cordia alliodora	71	59	0.295	0.355	0.416	-0.098	-0.037	0.026	-0.048	0.007	0.063	-0.086	-0.027	0.033	-0.166	-0.119	-0.073
Cordia bicolor	92	63	0.343	0.389	0.436	-0.085	-0.018	0.051	-0.053	-0.005	0.044	-0.060	-0.007	0.044	-0.135	-0.080	-0.024
Cordia lasiocalyx	177	108	0.308	0.345	0.385	-0.037	-0.006	0.025	-0.043	-0.015	0.013	-0.012	0.013	0.037	-0.125	-0.093	-0.061
Coussarea curvigemmia	210	129	0.192	0.225	0.257	-0.070	-0.034	0.003	-0.044	-0.014	0.017	-0.015	0.013	0.042	-0.086	-0.054	-0.023
Croton billbergianus	66	32	0.477	0.541	0.604				-0.067	0.001	0.071	-0.063	-0.018	0.027	-0.112	-0.073	-0.035
Cupania rufescens	56	29	0.125	0.200	0.277				-0.079	-0.019	0.043	-0.047	-0.002	0.043	-0.190	-0.082	0.027
Desmopsis panamensis	893	577	0.245	0.264	0.283	-0.015	0.003	0.021	-0.012	0.004	0.019	-0.025	-0.008	0.008	-0.073	-0.059	-0.046
Drypetes standleyi	278	134	0.284	0.319	0.355	-0.025	0.010	0.046	-0.037	-0.011	0.014	-0.030	-0.006	0.017	-0.101	-0.074	-0.047
Erythroxylum macrophyllum	146	78	0.160	0.205	0.251	-0.062	-0.008	0.046	-0.021	0.036	0.093	-0.001	0.033	0.068	-0.101	-0.051	-0.001
Eugenia coloradoensis	112	56	0.260	0.312	0.367	-0.072	-0.017	0.038	-0.037	-0.004	0.029	-0.022	0.010	0.042	-0.153	-0.109	-0.066
Eugenia galalonensis	306	217	0.249	0.279	0.309	-0.048	-0.015	0.017	-0.034	-0.004	0.026	-0.022	0.002	0.027	-0.078	-0.056	-0.035
Eugenia nesiotica	134	94	0.290	0.359	0.428	-0.066	-0.019	0.030	-0.065	0.000	0.065	-0.012	0.023	0.057	-0.175	-0.131	-0.087

Eugenia oerstediana	2265	1345	0.279	0.294	0.308	-0.020	-0.007	0.005	-0.017	-0.006	0.006	-0.017	-0.005	0.007	-0.111	-0.100	-0.089
Faramea occidentalis	10980	5442	0.185	0.196	0.207	**-0.021**	**-0.015**	**-0.009**	-0.004	0.001	0.007	-0.016	-0.006	0.004	-0.075	-0.069	-0.064
Garcinia intermedia	682	460	0.147	0.168	0.189	-0.024	-0.005	0.015	-0.015	0.002	0.019	-0.012	0.006	0.024	-0.028	-0.013	0.001
Guapira standleyana	149	79	0.211	0.261	0.309	-0.048	-0.001	0.047	**0.018**	**0.057**	**0.097**	-0.031	0.003	0.036	-0.184	-0.131	-0.079
Guarea bullata	87	49	0.123	0.185	0.247				-0.077	-0.011	0.052	**-0.075**	**-0.039**	**-0.002**	-0.013	0.032	0.076
Guarea guidonia	462	255	0.183	0.207	0.231	**-0.054**	**-0.032**	**-0.011**	-0.028	-0.006	0.017	-0.035	-0.017	0.002	-0.084	-0.061	-0.038
Gustavia superba	650	374	0.139	0.158	0.178	-0.029	-0.007	0.015	-0.039	-0.018	0.002	-0.024	-0.007	0.011	-0.070	-0.048	-0.026
Hampea appendiculata	51	27	0.330	0.399	0.468				-0.090	-0.001	0.087	-0.104	-0.039	0.027	-0.140	-0.086	-0.033
Heisteria acuminata	139	74	0.181	0.228	0.273	-0.089	-0.044	0.001	-0.051	-0.015	0.021	-0.022	0.009	0.040	-0.147	-0.101	-0.056
Heisteria concinna	897	643	0.191	0.212	0.233	-0.023	-0.004	0.016	-0.020	-0.005	0.009	-0.011	0.006	0.022	-0.079	-0.055	-0.032
Hirtella triandra	329	224	0.321	0.348	0.376	-0.006	0.021	0.048	-0.017	0.004	0.026	-0.024	-0.001	0.022	-0.135	-0.110	-0.085
Hybanthus prunifolius	7384	4775	0.212	0.224	0.236	**-0.039**	**-0.031**	**-0.024**	-0.012	-0.004	0.004	**0.002**	**0.012**	**0.023**	-0.089	-0.083	-0.077
Inga marginata	1757	1049	0.246	0.262	0.278	**-0.030**	**-0.015**	**-0.001**	-0.023	-0.009	0.006	-0.008	0.005	0.019	-0.076	-0.063	-0.051
Inga multijuga	61	33	0.198	0.280	0.361				-0.045	0.108	0.267	-0.056	-0.008	0.040	-0.105	-0.061	-0.018
Inga nobilis	63	34	0.128	0.205	0.281				-0.055	-0.006	0.043	-0.030	0.009	0.046	-0.088	-0.030	0.028
Inga umbellifera	95	46	0.183	0.239	0.294				-0.040	0.002	0.044	-0.039	-0.005	0.030	-0.113	-0.048	0.012
Lacistema aggregatum	84	49	0.284	0.372	0.462				-0.119	0.001	0.123	-0.080	-0.031	0.019	-0.118	-0.082	-0.046
Lonchocarpus heptaphyllus	95	47	0.231	0.274	0.318				-0.026	0.014	0.055	-0.015	0.021	0.057	-0.101	-0.058	-0.017
Malpighia romeroana	65	35	0.170	0.243	0.316				-0.254	-0.080	0.095	-0.043	0.002	0.047	-0.176	-0.109	-0.043
Mouriri myrtilloides	1792	1035	0.297	0.314	0.331	-0.019	-0.005	0.009	-0.009	0.003	0.014	**-0.031**	**-0.018**	**-0.004**	-0.093	-0.082	-0.071
Nectandra lineata	264	193	0.245	0.280	0.314	-0.042	-0.011	0.021	-0.036	-0.005	0.027	-0.037	-0.011	0.016	-0.058	-0.025	0.008
Ocotea puberula	160	97	0.201	0.239	0.279	-0.058	-0.008	0.042	-0.025	0.001	0.027	-0.011	0.023	0.056	-0.090	-0.052	-0.015
Ocotea whitei	171	105	0.156	0.268	0.380	-0.032	-0.006	0.021	-0.090	-0.034	0.022	-0.037	-0.011	0.015	-0.146	-0.084	-0.023
Oenocarpus mapora	92	68	-0.158	-0.007	0.142	-0.033	0.038	0.109	-0.077	-0.026	0.025	-0.031	0.023	0.076	-0.149	-0.082	-0.015
Ouratea lucens	222	126	0.138	0.177	0.216	-0.038	-0.004	0.030	-0.023	0.009	0.040	-0.048	-0.024	0.000	-0.104	-0.071	-0.039
Picramnia latifolia	271	143	0.251	0.281	0.312	-0.006	0.022	0.050	-0.052	-0.024	0.002	-0.015	0.007	0.029	-0.097	-0.072	-0.048
Piper darienense	218	110	0.175	0.224	0.272	-0.035	0.009	0.053	-0.019	0.018	0.056	-0.051	-0.017	0.016	-0.137	-0.100	-0.063
Poulsenia armata	79	52	0.221	0.309	0.398	-0.080	-0.008	0.065	-0.095	-0.008	0.080	-0.066	-0.019	0.028	-0.166	-0.112	-0.059
Pouteria reticulata	715	416	0.206	0.225	0.245	-0.024	-0.006	0.012	-0.008	0.008	0.024	-0.015	0.000	0.014	-0.069	-0.045	-0.022
Protium tenuifolium	357	218	0.281	0.309	0.338	-0.039	-0.015	0.009	-0.038	-0.011	0.015	-0.011	0.008	0.026	-0.088	-0.068	-0.049
Psychotria acuminata	50	30	0.461	0.547	0.631				-0.050	0.031	0.109	-0.055	0.001	0.056	-0.188	-0.143	-0.098
Psychotria deflexa	71	48	0.357	0.426	0.496				-0.006	0.069	0.145	-0.065	-0.015	0.034	-0.130	-0.091	-0.050

Psychotria hoffmannseggiana	421	250	0.445	0.469	0.494	-0.049	-0.019	0.012	-0.025	-0.002	0.021	-0.022	0.000	0.023	-0.108	-0.093	-0.079
Psychotria horizontalis	1709	930	0.193	0.213	0.233	**-0.042**	**-0.027**	**-0.011**	-0.028	-0.014	0.001	-0.013	0.001	0.015	-0.132	-0.120	-0.109
Psychotria limonensis	55	20	0.297	0.371	0.445				-0.048	0.009	0.065	-0.036	0.007	0.051	-0.102	-0.055	-0.008
Psychotria marginata	227	127	0.282	0.321	0.361	-0.052	-0.005	0.040	-0.036	0.007	0.049	-0.035	-0.007	0.020	-0.103	-0.081	-0.059
Psychotria racemosa	128	111	0.347	0.401	0.456	-0.097	-0.023	0.051	**0.004**	**0.057**	**0.109**	-0.107	-0.043	0.019	-0.130	-0.095	-0.061
Quararibea asterolepis	2652	1430	0.221	0.235	0.249	-0.020	-0.009	0.001	-0.020	-0.009	0.002	-0.008	0.004	0.015	-0.115	-0.103	-0.091
Randia armata	5024	2926	0.132	0.145	0.159	-0.008	0.000	0.008	-0.009	-0.001	0.008	-0.007	0.003	0.014	-0.160	-0.149	-0.138
Rinorea sylvatica	423	226	0.208	0.236	0.264	-0.027	0.000	0.028	-0.036	-0.008	0.021	-0.027	-0.006	0.014	-0.106	-0.085	-0.064
Senna dariensis	68	41	0.327	0.385	0.443				-0.090	-0.016	0.059	-0.049	-0.003	0.045	-0.151	-0.104	-0.056
Simarouba amara	173	70	0.344	0.384	0.424	-0.005	0.034	0.072	-0.050	-0.022	0.006	**-0.048**	**-0.024**	**0.000**	-0.105	-0.073	-0.042
Sorocea affinis	1113	679	0.231	0.250	0.268	-0.023	-0.006	0.011	-0.011	0.003	0.018	-0.014	0.001	0.016	-0.118	-0.101	-0.083
Strychnos brachistantha	51	37	0.032	0.186	0.342				-0.078	-0.004	0.069	-0.088	-0.020	0.048	-0.358	-0.084	0.187
Stylogyne turbacensis	364	170	0.113	0.151	0.189	-0.053	-0.022	0.008	-0.012	0.014	0.041	-0.026	-0.002	0.022	-0.127	-0.098	-0.070
Swartzia simplex var.grandiflora	350	229	0.199	0.235	0.273	-0.018	0.014	0.046	-0.030	-0.002	0.025	-0.030	-0.008	0.014	-0.148	-0.109	-0.072
Swartzia simplex var.ochnacea	87	45	0.168	0.249	0.333				-0.105	-0.037	0.031	-0.015	0.017	0.050	-0.194	-0.129	-0.066
Tabebuia rosea	125	81	0.311	0.362	0.413	-0.090	-0.035	0.019	-0.059	-0.018	0.021	-0.040	0.007	0.054	-0.106	-0.065	-0.026
Tabernaemontana arborea	123	63	0.248	0.305	0.361	-0.004	0.046	0.095	-0.066	-0.009	0.047	-0.049	-0.016	0.016	-0.111	-0.075	-0.041
Tachigali versicolor	124	76	0.269	0.335	0.399	**-0.076**	**-0.039**	**-0.001**	-0.058	0.032	0.122	**-0.060**	**-0.034**	**-0.007**	-0.102	-0.066	-0.030
Talisia nervosa	67	41	0.164	0.232	0.300				-0.040	-0.008	0.024	-0.076	-0.029	0.016	-0.164	-0.090	-0.014
Tetragastris panamensis	1109	623	0.238	0.254	0.271	-0.018	-0.004	0.010	0.000	0.011	0.022	-0.014	-0.002	0.011	-0.059	-0.045	-0.032
Trichilia pallida	87	40	0.216	0.275	0.331				-0.024	0.024	0.072	-0.015	0.029	0.072	-0.148	-0.086	-0.025
Trichilia tuberculata	7381	2901	0.183	0.194	0.206	-0.012	-0.004	0.003	-0.003	0.003	0.009	-0.014	-0.004	0.006	-0.060	-0.053	-0.047
Triplaris cumingiana	220	148	0.124	0.171	0.217	**-0.080**	**-0.049**	**-0.018**	-0.042	-0.007	0.027	-0.023	0.004	0.032	-0.203	-0.152	-0.102
Trophis caucana	73	53	0.186	0.274	0.362	-0.047	0.015	0.078	-0.144	-0.043	0.058	-0.066	-0.009	0.048	-0.205	-0.136	-0.067
Unonopsis pittieri	109	86	0.297	0.355	0.414	**-0.133**	**-0.072**	**-0.010**	-0.039	0.009	0.056	-0.047	0.001	0.049	-0.268	-0.194	-0.121
Virola sebifera	134	94	0.208	0.251	0.294	-0.070	-0.010	0.050	-0.074	-0.027	0.020	-0.047	0.000	0.046	-0.112	-0.051	0.009
Vochysia ferruginea	58	47	0.378	0.508	0.640				-0.187	-0.091	0.004	**-0.160**	**-0.089**	**-0.017**	-0.170	-0.109	-0.047

Table S2 Mean and 95% CI of responses in terms of first-year survival to shade (β1), spatial drought (β2) and inter-annual drought (β3) for all species. Further shown are the number of observations of a species in years with and without shade estimates, the survival constant (β0) and the response to ln(height) (β4). Bold and underlined values indicate significant responses to shade or drought, i.e. the 95% credible interval (CI) excluded zero. Underlined values indicate that the CI of β0 or β4 excluded zero.

	Observations		Mean RGR (β0)			Shade (β1)			Spatial drought (β2)			Int.-an. drought (β3)			ln(height) (β4)		
Species	all	shade	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+	CI-	mean	CI+
Acalypha diversifolia	104	56	0.445	1.105	1.844				**-0.963**	**-0.484**	**-0.031**	**-1.620**	**-1.002**	**-0.429**	0.389	0.798	1.266
Aegiphila panamensis	172	143	-1.183	-0.697	-0.213	-0.304	0.277	0.867	-0.189	0.224	0.644	-0.539	-0.026	0.459	0.604	1.246	1.939
Apeiba membranacea	119	75	-2.852	-1.917	-1.091				-1.068	-0.336	0.331	-0.719	0.051	0.798	0.229	0.861	1.577
Beilschmiedia pendula	1782	1428	-2.086	-1.694	-1.321	-0.050	0.071	0.191	**-0.279**	**-0.141**	**-0.002**	-0.172	-0.002	0.171	0.702	0.894	1.092
Capparis frondosa	218	131	0.424	0.767	1.118	-0.383	0.040	0.475	-0.437	-0.088	0.274	-0.689	-0.312	0.065	0.448	0.943	1.475
Cecropia insignis	166	115	-2.835	-2.188	-1.627	-0.249	0.502	1.321	-0.210	0.257	0.698	**-1.952**	**-1.056**	**-0.237**	0.218	0.568	0.953
Chrysophyllum cainito	220	91	-0.030	0.431	0.909				**0.065**	**0.396**	**0.727**	-0.295	0.079	0.476	-0.336	0.207	0.755
Cinnamomum triplinerve	101	44	-1.570	-0.809	-0.103				-0.388	0.081	0.525	-0.332	0.115	0.578	-0.223	0.453	1.218
Coussarea curvigemmia	129	87	-0.741	-0.321	0.100				-0.422	-0.056	0.301	-0.779	-0.125	0.523	-0.534	0.322	1.218
Dendropanax arboreus	180	105	-2.667	-1.234	0.150	-0.663	-0.008	0.650	-0.736	-0.211	0.273	**-1.241**	**-0.632**	**-0.078**	-0.058	0.868	1.830
Desmopsis panamensis	333	258	0.408	0.719	1.042	-0.637	-0.317	0.002	-0.240	0.039	0.318	-0.210	0.145	0.503	0.697	1.121	1.584
Eugenia oerstediana	836	398	0.046	0.230	0.415	-0.320	-0.066	0.183	-0.165	0.008	0.183	-0.243	-0.059	0.121	0.434	0.699	0.973
Faramea occidentalis	6110	2348	-0.431	-0.302	-0.176	-0.104	0.003	0.111	**-0.172**	**-0.096**	**-0.019**	**-0.277**	**-0.157**	**-0.037**	0.753	0.842	0.933
Guapira standleyana	164	82	-0.959	-0.601	-0.248				-0.222	0.120	0.454	-0.543	-0.164	0.203	-0.391	0.033	0.455
Guarea guidonia	178	108	-0.441	-0.031	0.375	-0.674	-0.201	0.282	**-0.768**	**-0.439**	**-0.120**	-0.524	-0.182	0.164	0.031	0.706	1.405
Gustavia superba	348	169	-0.451	-0.096	0.264	-0.024	0.337	0.709	-0.265	-0.006	0.257	-0.469	-0.176	0.116	0.295	0.578	0.860
Hampea appendiculata	100	65	-2.460	-1.616	-0.882				-0.913	-0.166	0.590	-1.362	-0.531	0.282	0.450	1.604	2.840
Heisteria concinna	487	323	-0.319	-0.042	0.228	-0.057	0.192	0.442	**0.002**	**0.193**	**0.385**	-0.426	-0.195	0.038	0.234	0.637	1.042
Hirtella triandra	214	137	-1.742	-1.203	-0.700	-0.215	0.193	0.602	-0.313	0.012	0.331	-0.513	-0.170	0.172	0.864	1.360	1.898
Hybanthus prunifolius	5661	3789	-0.117	0.016	0.149	**-0.256**	**-0.163**	**-0.072**	-0.074	0.014	0.100	**-0.244**	**-0.129**	**-0.014**	0.935	1.044	1.154
Inga marginata	567	305	0.117	0.371	0.629	-0.261	0.001	0.264	-0.351	-0.151	0.051	-0.226	0.002	0.230	0.426	0.772	1.138
Jacaranda copaia	159	86	-6.137	-4.062	-2.537				-0.902	0.738	2.577	-3.335	-1.230	0.608	-0.179	1.083	2.435
Luehea seemannii	165	27	-2.191	-1.433	-0.763				-0.656	0.093	0.878	-0.779	-0.214	0.358	0.202	0.529	0.889
Miconia argentea	115	87	-1.226	-0.662	-0.109				-0.704	-0.173	0.303	-1.203	-0.546	0.071	0.320	0.638	0.993
Mouriri myrtilloides	488	285	-0.784	-0.506	-0.235	-0.151	0.121	0.395	-0.218	-0.029	0.162	-0.238	-0.013	0.211	1.218	1.659	2.119
Ocotea puberula	232	147	-1.110	-0.762	-0.422	-0.310	0.132	0.584	-0.058	0.220	0.492	-0.483	-0.174	0.129	-0.016	0.729	1.502

Ocotea whitei	169	109	-6.022	-3.775	-1.713	-0.250	0.118	0.491	-0.424	0.360	1.136	**-1.095**	**-0.616**	**-0.164**	0.603	1.247	1.945
Piper reticulatum	151	65	-1.904	-0.987	-0.112				-0.541	0.035	0.585	**-1.057**	**-0.573**	**-0.127**	-0.059	0.388	0.842
Pouteria reticulata	331	153	-1.585	-0.764	0.000	-0.060	0.302	0.671	-0.373	-0.105	0.158	**-0.689**	**-0.429**	**-0.173**	0.312	0.914	1.554
Protium tenuifolium	117	46	-0.913	-0.041	0.785				-0.534	-0.080	0.358	-0.842	-0.397	0.025	-0.270	0.534	1.444
Psychotria hoffmannseggiana	345	210	-0.231	0.093	0.434	-0.503	-0.182	0.132	-0.304	-0.054	0.189	-0.556	-0.260	0.031	0.562	0.862	1.172
Psychotria horizontalis	1315	788	0.173	0.447	0.730	**-0.377**	**-0.200**	**-0.025**	-0.264	-0.124	0.016	-0.193	-0.031	0.130	0.599	0.759	0.926
Psychotria marginata	191	126	-0.493	0.286	1.072	-1.059	-0.511	0.037	-0.523	-0.095	0.325	-0.351	0.056	0.461	0.349	0.772	1.215
Quararibea asterolepis	1299	931	-0.745	-0.559	-0.379	-0.268	-0.105	0.052	-0.055	0.096	0.246	-0.148	0.018	0.186	0.696	0.883	1.076
Randia armata	2467	1217	-0.173	-0.036	0.107	**0.107**	**0.248**	**0.390**	-0.088	0.021	0.133	**-0.335**	**-0.197**	**-0.061**	0.667	0.830	0.995
Rinorea sylvatica	183	83	-0.142	0.435	1.013				-0.289	0.134	0.555	-0.245	0.334	0.939	0.561	1.173	1.852
Senna dariensis	178	136	-1.576	-1.029	-0.485	**0.034**	**0.662**	**1.342**	-1.032	-0.372	0.263	-0.789	-0.255	0.277	0.640	1.416	2.282
Sorocea affinis	604	330	-0.462	-0.252	-0.042	-0.033	0.213	0.460	-0.123	0.058	0.240	-0.268	-0.057	0.156	0.375	0.677	0.997
Stylogyne turbacensis	137	55	-0.061	0.668	1.443				-0.325	-0.009	0.308	-0.593	-0.234	0.121	-0.135	0.434	1.029
Tabebuia rosea	133	76	-2.079	-1.403	-0.776				-0.192	0.181	0.560	-0.300	0.298	0.927	0.924	1.658	2.461
Tetragastris panamensis	570	308	-1.965	-1.392	-0.836	-0.359	-0.053	0.247	-0.074	0.118	0.315	-0.270	-0.083	0.100	0.705	1.143	1.612
Trichilia tuberculata	3650	773	-0.298	-0.153	-0.008	**-0.342**	**-0.184**	**-0.023**	-0.159	-0.070	0.019	-0.130	0.004	0.137	0.877	1.014	1.155
Triplaris cumingiana	151	93	-0.337	0.105	0.549				-0.324	0.082	0.489	-0.165	0.246	0.661	0.605	1.322	2.102
Trophis caucana	101	75	-1.944	-1.164	-0.439				-0.934	-0.177	0.548	**-1.437**	**-0.832**	**-0.274**	-0.474	0.261	1.012
Virola sebifera	120	67	-2.239	-1.423	-0.688				-0.535	-0.068	0.389	-0.934	-0.413	0.084	0.526	1.323	2.219